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In Cooperation with the
Illinois, Kansas, North Carolina, Oregon, Washington, and
Wisconsin Agricultural Experiment Stations

DEPARTMENT BULLETIN No. 1347

Washington, D. C. ▼ November, 1925

FOOT-ROT DISEASES OF WHEAT IN AMERICA

By

HAROLD H. McKINNEY, Pathologist
Office of Cereal Investigations, Bureau of Plant Industry

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By HAROLD H. MCKINNEY,[1] *Pathologist, Office of Cereal Investigations, Bureau of Plant Industry*

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INTRODUCTION

It is the purpose in this bulletin to bring together in a general way the more important information now in hand concerning the foot-rot diseases of wheat as they occur in this country and to discuss the status of these diseases as set forth in the foreign literature in so far as it may throw light on our own problems. Although further study is required before these diseases are fully understood, it has been possible during the past five years to obtain data and make observations which assist considerably in the matter of clarifying some of the problems involved in the general problem of wheat foot-rots.

A study of the literature indicates that the foot-rot diseases of wheat are practically world-wide with the wheat crop. They are reported from continental Europe, Australia, England, the Orient, South America, Africa, and the United States. As far as known, Cordley (*14*)[2] was the first to report a definite foot-rot in this country. In 1902 he reported one of these diseases on wheat in Oregon, but he did not determine the species of fungus associated with it. This report attracted little or no attention from plant pathologists, and it was not until the discovery of wheat rosette (*32*, *44*) in 1919 (then thought to be the take-all disease) that general attention was directed to the importance of the foot-rot diseases. Since that time several of the European wheat foot-rots have been found to occur in this country, and as a result increasing interest is being shown in this group of diseases and also in the similar diseases which Bolley (*8*, *9*, *10*) and his associates (*4*) pointed out some years ago in connection with the general deterioration of wheatlands in the spring-wheat region.

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[1] The writer wishes to acknowledge the helpful suggestions given by J. J. Davis and E. M. Gilbert, of the University of Wisconsin, and by C. L. Shear, of the U. S. Department of Agriculture, in connection with the mycological phases of this bulletin.

[2] The serial numbers (*italic*) in parentheses refer to "Literature cited," at the end of this bulletin.

USE OF THE TERM "FOOT-ROT"

From the foreign literature and from conferences with foreign workers who have visited America recently, it seems apparent that the term "foot-rot," or its foreign equivalents, as generally used on the Continent of Europe, applies to a set of more or less similar plant symptoms which appear to be caused by one or more fungous parasites. A study of the literature indicates, however, that this term has been applied most frequently to the disease caused by *Ophiobolus graminis* Sacc. and to those said to be caused by *O. herpotrichus* (Fr.) Sacc., *Leptosphaeria herpotrichoides* De Not, and *L. culmifraga* (Fr.) Ces. and De not. The term "foot-rot" has been used by most foreign workers to designate a rotting or shriveling and blackening or browning of the roots and the basal portion of the culms and the crown of wheat plants which have advanced beyond the seedling stage. In fact, the foreign literature dealing with the foot-rots gives very little information concerning seedling injury.

In the United States Cordley (*14*), Dana (*15*), and McKinney and Melchers (*48*) have followed the European practice of applying the term "foot-rot" to diseased wheat plants which had advanced well toward maturity, and in all these cases the diseases dealt with resembled the foot-rot caused by *Ophiobolus graminis* and the foot-rots which have been described in connection with *O. herpotrichus* and *Leptosphaeria herpotrichoides.* Atanasoff (*1*), working with the wheat malady caused by *Gibberella saubinetii*, also applied the term "foot-rot" to that disease as it occurs on the base and roots of plants well advanced in development. Drechsler (*19*), in his studies of grass diseases caused by species of Helminthosporium, used the term "foot-rot" in the same sense as Atanasoff. On the other hand, Stevens (*66*, *67*), working with the wheat disease caused by *Helminthosporium sativum*,[3] applied the name "foot-rot" to the diseased base and roots of young seedlings and to older wheat plants as well. His usage of the term includes the diseased condition which most workers, Atanasoff (*1*), Johnson (*35*), Johnson and Dickson (*34*), Dickson (*18*), McKinney (*45*), Stakman (*65*), Weniger (*74*), and others, have designated as seedling blight. His usage also confused Helminthosporium seedling blight with the rosette disease.

In view of the number of parasites causing wheat foot-rots and owing to the similarity in many cases between symptoms of these diseases, it becomes rather difficult to develop a system of common names which will be entirely satisfactory from every standpoint; in fact, the lack of knowledge concerning these diseases makes it impracticable to attempt to work out a detailed system at the present time. As pointed out, previous workers have already started what seems to be a rational system, and it seems well to follow this in a general way to avoid unnecessary confusion in the literature.

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[3] The writer has examined cultures of this Helminthosporium which Doctor Stevens kindly supplied, and it is very evident that the organism is *Helminthosporium sativum* P., K., and B.

Accordingly the term "foot-rot," as used in this bulletin, designates a rotting or serious infection of any part of or the entire basal portion of wheat plants which have advanced beyond the seedling[4] stage. The term thus includes a basal culm or stalk rot, crown-rot, and root-rot, occurring separately or together, which may be caused by any parasite.

The term "seedling blight" is used, as it has been by the workers previously mentioned, to designate a severe injury or killing of the seedling and includes the complete blighting or partial discoloration of the leaves as well as stem-rot and root-rot caused by any parasite.

While this bulletin deals primarily with the foot-rot diseases, other manifestations than foot-rot are considered incidentally in the sections dealing with parasites which attack all parts of the plant.

TAKE-ALL, THE FOOT-ROT CAUSED BY OPHIOBOLUS GRAMINIS

COMMON NAMES

Straw blight, England. Smith (*64*), 1884.
Foot disease (maladie du pied), France. Prillieux and Delacroix (*57*), 1890.
Foot-rot (piétin), France. Schribaux (*63*), 1892.
Black-foot (pied noir), France. Gaillot (*25*), 1897.
Die-back disease (tachigare-byo) and white wilt, Japan. Hori (*31*), 1901.
Take-all and white-heads, Australia. McAlpine (*41*), 1904.

Several other names have been associated with this type of disease, but in these cases it is not clear that *Ophiobolus graminis* Sacc. was the cause. Also, some of the names mentioned evidently were applied to the disease before *O. graminis* was found associated with it, as is undoubtedly the case with the names straw blight, take-all, and white-heads. It seems evident that the name "take-all" was not the first one applied to the disease caused by *O. graminis*, but, as priority is not always adhered to in deciding the usage of common names of diseases, this name is used because it is the most common among English-speaking people and is the one now accepted in this country.

GEOGRAPHIC DISTRIBUTION

Take-all was first found in the United States (*62*) in 1919 near Roanoke, Va. These diseased wheat plants were sent to the Office of Cereal Investigations of the United States Department of Agriculture on June 16 by Dr. F. D. Fromme. Later the plants were examined and mature perithecia of *Ophiobolus graminis* were found on them.[5] Since 1919 this disease has been found in several new locations, until now it is known to occur in most of the winter-wheat areas in this country. Locations where the disease has been found and relevant information are given in Table 1, and the locations are shown in Figure 1. These show that the disease is well distributed throughout the United States, thus making it practically impossible to get accurate information concerning its origin. Indications are that the disease has not been introduced recently, but rather that it existed here for many years before being observed. The more extensive distribution of the disease in western New York might be taken as an indication that it was first introduced there, but this can hardly be assumed, as it is entirely possible that infested material may have been introduced at several points at different times from different parts of the world.

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[4] The term "seedling" as here used applies to the young plant before it has developed its permanent root system.

[5] This fungus was identified by R. W. Goss, A. G. Johnson, and the writer.

TABLE 1.—*Distribution of take-all caused by Ophiobolus graminis in the United States*

[The sources of information for items marked with an asterisk (*) are the various reports of the Office of Plant-Disease Survey of the United States Department of Agriculture]

Year	State and county	Collector	Organism identified by—
	ARKANSAS		
*1921	Washington	H. R. Rosen	H. R. Rosen and J. A. Elliott.
	CALIFORNIA		
1923	Yolo	H. B. Humphrey and W. W. Mackie.	H. B. Humphrey and W. T Horne.
	INDIANA		
*1921	Knox		H. S. Jackson.
	KANSAS		
1922–1923	Dickinson	L. E. Melchers and the writer	H. Fellows, R. P. White, and the writer.
*1923	Rice		L. E. Melchers and R. P. White.
1923	Shawnee		R. P. White.
1923	Riley	L. E. Melchers and the writer	H. Fellows, R. P. White, and the writer.
	MARYLAND		
1922	Kent	A. G. McCall	J. B. S. Norton and A. G. Johnson.
	NEW YORK		
*1921–1923	Cayuga	R. S. Kirby and others	R. S. Kirby and others.
*1921, 1923	Cortland	do	Do.
*1922	Erie	do	Do.
*1920–1923	Genesee	do	Do.
*1921–1923	Livingston	do	Do.
*1921	Madison	do	Do.
*1921–1923	Monroe	do	Do.
*1921	Oneida	do	Do.
*1921, 1923	Onondaga	do	Do.
*1921, 1923	Ontario	do	Do.
*1922	Orleans	do	Do.
*1921, 1923	Oswego	do	Do.
*1921	Schuyler	do	Do.
*1921–1923	Seneca	do	Do.
*1921–1923	Tompkins	do	Do.
*1921–1923	Wayne	do	Do.
*1921	Wyoming	do	Do.
*1921	Yates	do	Do.
	NORTH CAROLINA		
1923	Alexander	F. A. Wolf and G. W. Fant	F. A. Wolf.
1923	Cabarrus	do	Do.
1923	Iredell	do	Do.
1923	Lincoln	F. A. Wolf	A. G. Johnson.
	OREGON		
*1921–1923	Benton	H. P. Barss, M. B. McKay, A. G. Johnson, and H. Fellows.	H. P. Barss, M. B. McKay, A. G. Johnson, and H. Fellows.
*1921	Hood River		H. P. Barss.
*1921	Lane		Do.
*1921	Washington		Do.
1923	Clackamas	H. Fellows	H. Fellows.
	TENNESSEE		
*1923	Knox	C. D. Sherbakoff and H. B. Humphrey.	C. D. Sherbakoff and H. B. Humphrey.
	VIRGINIA		
1919	Roanoke	F. D. Fromme	R. W. Goss, A. G. Johnson, and the writer.

As yet the disease has not been found in the hard spring-wheat belt of the United States. Fraser (*24*), however, in 1923 found the disease severe in one field of Marquis (spring) wheat in Saskatchewan, Canada. Davis[6] found Marquis susceptible to infection by *Ophiobolus graminis.* He also found that this variety became badly infected when sown in infested soil in the spring out of doors at Madison, Wis. These plats were inoculated with a pure culture of the parasite the previous fall and subjected to outside conditions during the entire winter. It is evident, therefore, that take-all will develop in the spring-wheat region if the fungus is present.

Although the take-all infested areas occurring in this country are relatively small, it is important to note that as infection centers they are located at rather strategic points. The disease seems to have a firm hold in the center of the hard winter-wheat belt, and observations show that it is steadily spreading.

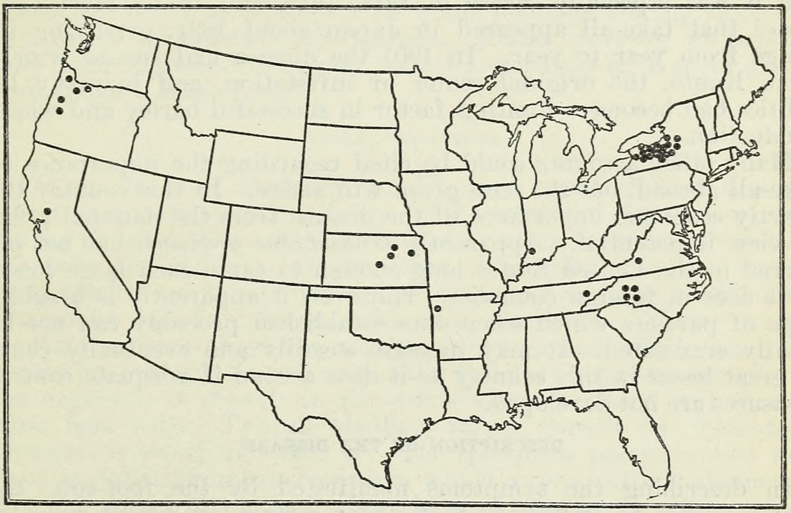

FIG. 1.—Outline map of the United States, showing locations, indicated by dots, where wheat take-all has been found

ECONOMIC IMPORTANCE

Take-all is capable of causing great losses in the United States by killing the plants outright or by producing badly shriveled grain. In fields where the disease is abundant it prevents successful wheat growing. In some regions it has not been uncommon to find fields where it caused a decrease of 50 to 60 per cent of the grain crop, and greater losses frequently occur. In this connection, H. P. Barss reported to the Office of Plant-Disease Survey that in 1921 he observed 50 acres of wheat in Oregon in which 10 acres were entirely destroyed by this disease and 20 acres were hardly worth harvesting. On the other hand, many of the infested fields observed have shown only a relatively small amount of infection, and owing to seasonal conditions the severity of the disease has increased or decreased from one season to another. It has been found, however, that where wheat follows wheat repeatedly on infested land, the take-all spots increase in size slowly but steadily, and newly infested areas become evident.

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[6] Davis, R. J. Studies on Ophiobolus graminis Sacc. and the Take-All Disease of Wheat. (Unpublished manuscript.)

In Australia McAlpine (*42*) states that take-all is more dreaded by farmers than rust, and Brittlebank (*11*) says: "Of all fungous diseases affecting wheat 'take-all' is the most destructive, and the actual loss caused by it is far greater than by any other single disease, rust included, or perhaps by a combination of all known fungous diseases affecting wheat in Victoria." Darnell-Smith (*16, pp. 25–27*) states that in New South Wales take-all reduces the wheat yield as much as 50 per cent in the affected fields. According to E. Foëx[7] take-all is of considerable economic importance in France, and it was especially severe in 1912, 1913, and 1914. Hori (*31*) states that take-all appeared in Japan about 1891, extending its range from year to year. In 1901 the disease had spread widely from Kanto, the original center of infestation, and in many localities had become a limiting factor in successful barley and wheat production.

Many other accounts could be cited regarding the importance of take-all abroad, but the ones given will suffice. In this country the strictly economic importance of the disease from the national point of view is potential. Apparently *Ophiobolus graminis* has not occurred in the United States long enough to cause such large losses as it does in foreign countries. However, it apparently is a subtle type of parasite which when once established probably can not be totally eradicated. It may increase steadily and eventually cause as great losses in this country as it does abroad if adequate control measures are not developed.

DESCRIPTION OF THE DISEASE

In describing the symptoms manifested by the foot-rots, the writer wishes to emphasize that under certain conditions some of these diseases are difficult to distinguish from each other. This is especially true in certain cases regarding general field appearances, such as spotting, and it is becoming more evident as our studies progress that gross plant symptoms, such as stunting, yellowing, bronzing, bleaching, and white-heads, are of much less value as diagnostic characters of the specific foot-rots than has been thought heretofore.

The fungus causing the take-all disease attacks all of the underground parts of the plant and parts near the soil line, but there is no evidence which indicates that *Ophiobolus graminis* attacks the leaves, heads, or parts of the stem which are some distance above the soil line. The symptoms manifested by these parts of diseased plants appear to be brought about wholly as a result of the destruction of the root system and basal portion of the affected plants.

FIELD APPEARANCE

The writer has never noted any conspicuous indication of take-all during the fall in fields of winter wheat. Occasionally a plant will show visible signs of attack at this time, but there is no outstanding manifestation of the disease even in areas known to be infested by the causal organism. In general, these observations seem to be in accord with those made by Hori (*31*), who has studied this disease on barley, wheat, and rye in Japan.

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[7] While on a visit to this country in 1920 Doctor Foëx very kindly gave the writer considerable information concerning the occurrence to foot-rots in France.

In the spring the disease may appear in large or small areas, and it frequently causes a spotting in fields, as shown in Plate I. Often many small spots are scattered throughout infested fields, giving them a very ragged appearance, as shown in Plate I, *B*. These spots are very conspicuous on account of the bleached-yellow or reddish yellow color of dead or dying plants. In some cases the diseased plants may break over at the base, but from the writer's experience this seems to be the exception rather than the rule. Frequently the disease may not appear until late in the development of the wheat plants, causing a bleaching of the whole plant, producing the condition called white-heads in Australia. Plants showing white-heads may occur in spots or they may be scattered singly or in small groups throughout a large area.

DISEASE SYMPTOMS

On the basis of the work of Davis it seems evident that the wheat plant may become infested by the take-all fungus at any time during its life. Although the work of Davis indicated that seedlings are more susceptible to infection than older plants grown under the same conditions, it is of interest to note that seedling blight is not commonly found under natural field conditions. Under experimental conditions, however, seedling infection and killing take place regularly, probably on account of the fact that a greater quantity of the organism is present in the artificially inoculated soil than in most field soils. Typical seedling injury caused by *Ophiobolus graminis* is shown in Plate II. The specimens photographed were from an inoculation experiment in which a pure culture of the fungus was added to the soil when the seed was sown. Older plants infected with the parasite under natural field conditions are shown in Plate III. It will be noted that the aboveground portions of the diseased plants show a bronze to yellow coloration. The underground portion of the tillers, the crown, and the roots show brown to black lesions or a general brown to black coloration and rotting. Close examination of the blackened areas will show the presence of a crust of interwoven mycelium ("mycelial plate;" Pl. IV, *A*). On the stems this crust occurs on and under the coleoptile and leaf sheaths and is attached to them or to the stem. Under certain conditions the small black perithecia (Pl. IV, *B* and *C*) of the parasite will be found on the inner side of the leaf sheaths with their beaks projecting through the outer surface. They may appear also on the roots. It is not uncommon, however, to find an abundance of disease in some localities without any development of perithecia on the affected plants. This condition also frequently occurs on diseased plants growing under pure-culture conditions where *O. graminis* is the only fungus present.

When plants are attacked after the seedling stage, they react in essentially the same manner as seedlings. In many cases the lower leaf sheaths of such plants are held together tightly and all the sheaths are held fast to the culm by the dense growth of interwoven mycelium.

Plants which are attacked during the middle of the summer growing period usually remain erect and stiff until cut down at harvest. However, cases have been noted where such plants break over at the base. When an attempt is made to pull the diseased plants out of the soil they frequently break off at the soil line, and when this breaking does not occur it will be found frequently that the root system is badly rotted.

When plants become infected or react to previous infection after the heading stage, the whole plant becomes bleached, and a whitehead condition results. Such heads produce no grain or grain which is of light weight, depending on the stage of seed development at the time the plant succumbs to the attack by the fungus.

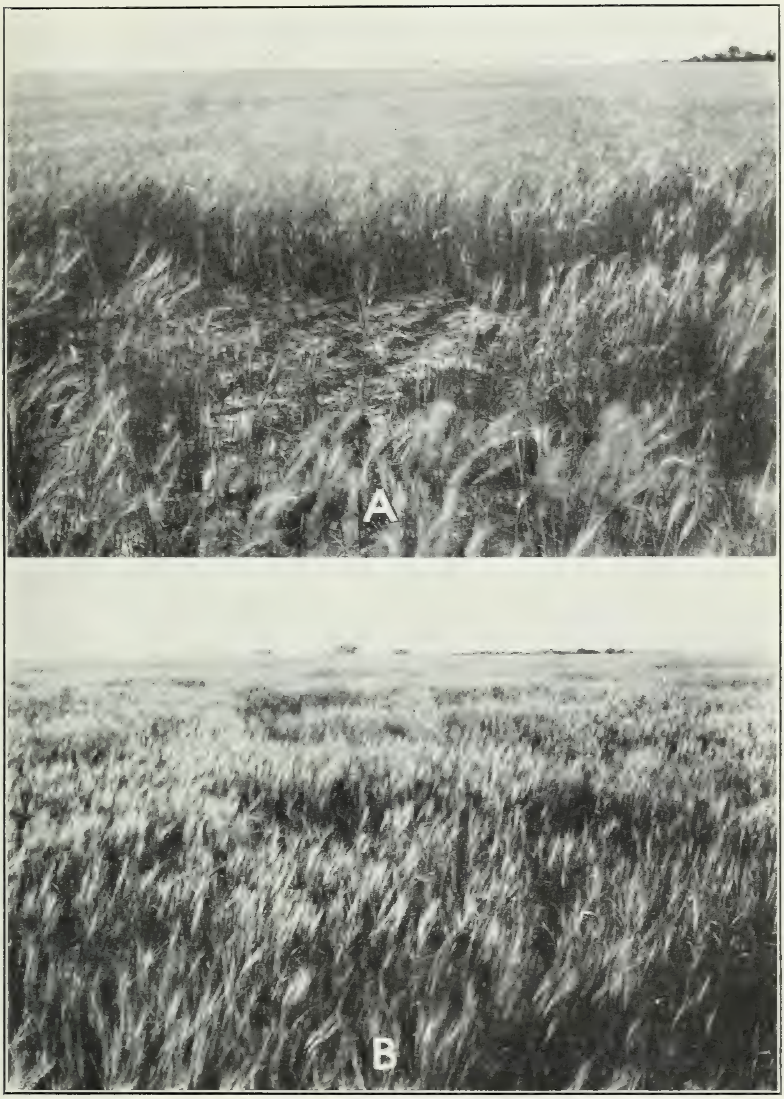
It is not uncommon to find plants showing only a mild root or culm infection without any apparent injury to the aboveground parts. In such cases the bases of the culms may show only a blackening, with no indication of tissue disintegration, and the roots will have but few lesions. It also is common upon removing dead plants from the soil to discover that their culms are perfectly clean and the root system completely rotted. Likewise there are cases where death is apparently due entirely to the rotting of the culms and crowns. In many cases some of the culms of a plant are killed and the others unaffected.

The writer has observed that a small percentage of experimental plants infected with *Ophiobolus graminis* tends to develop more of a brown than a black discoloration at the bases of the culms, a condition resembling the browning produced by *Helminthosporium sativum* and by *Gibberella saubinetii.* This browning, however, is seldom produced by *O. graminis* without some development of a black or dark-brown mycelial weft or plate on the browned parts of the plant, which plate is absent from the bases of plants attacked by *H. sativum* or *G. saubinetii.* In this connection, however, the writer does not wish to imply that *O. graminis* is the only wheat parasite that produces a mycelial plate.

CAUSE OF THE DISEASE

Take-all is caused by a sac fungus, which has been generally designated by the name *Ophiobolus graminis* Sacc. ever since pathologists recognized that this parasite is associated with this disease. It now appears, however, that certain workers doubt the validity of this binomial, and it may be well to present the available evidence bearing on the subject.

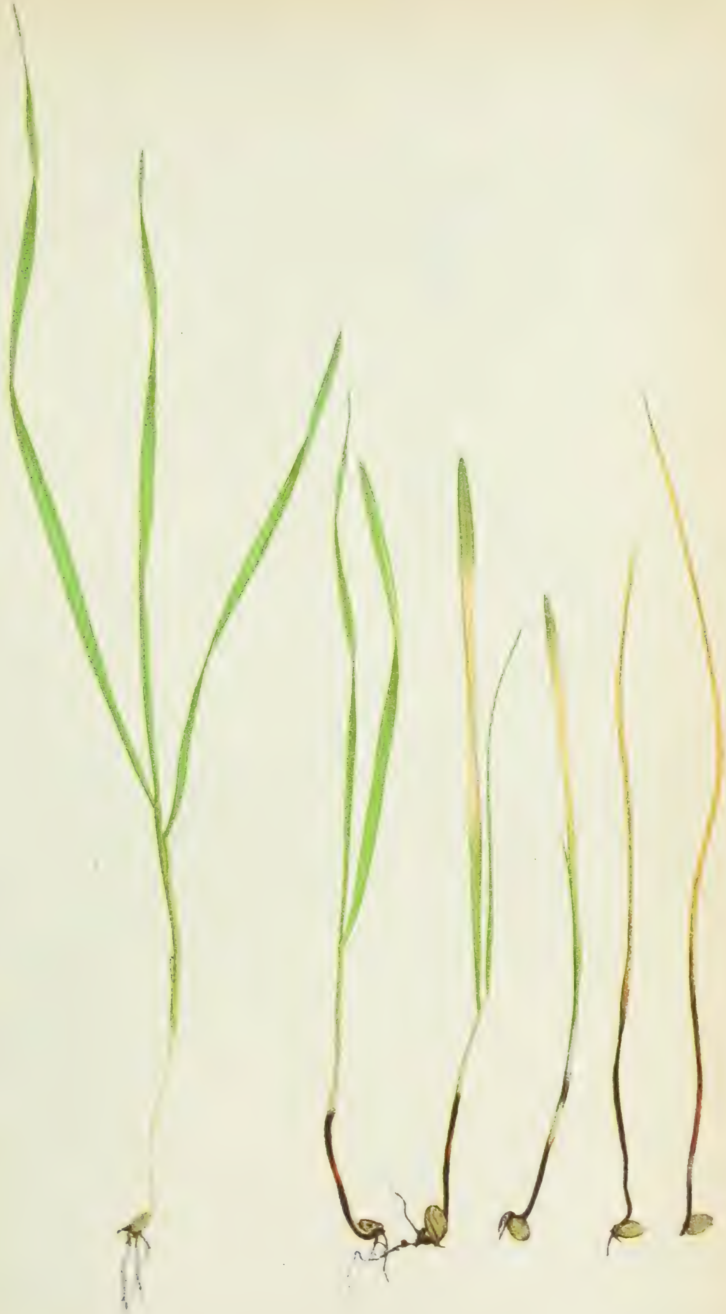
In going over the literature it appears that Berlese (*7, pp. 119–120*) made a study of certain species of Ophiobolus and reported that there are certain cases of synonymy. He compared the type specimens of *Ophiobolus eucryptus* (Berk. and Br.) Sacc., *O. cariceti* (Berk. and Br.) Sacc., and *O. graminis* Sacc. and found that they agreed. On the basis of these comparisons Berlese held that inasmuch as the name *O. eucryptus* antedated the other two by a number of years the latter names become invalid. Strangely enough, however, Berlese's interpretation was never generally accepted, and



Spots of Foot-Rot in Wheat Fields in Central Kansas

Photographed June 12, 1921

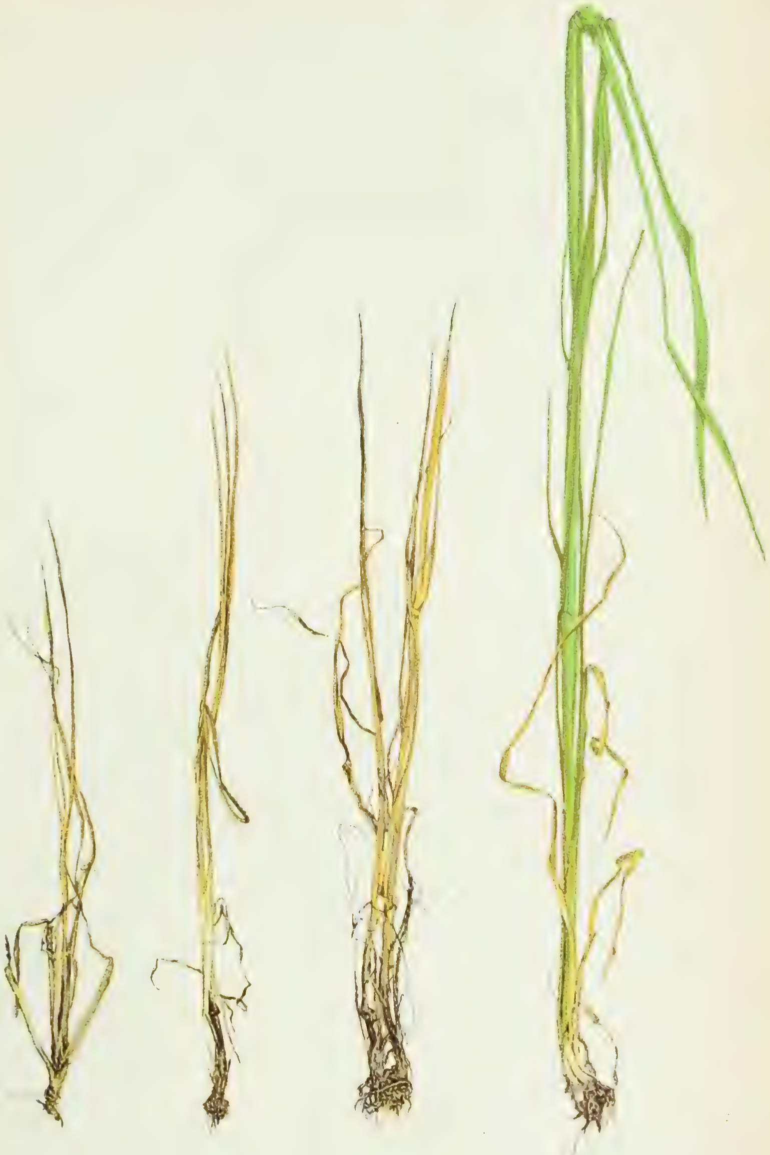
A, Foot-rot spot in a field of Turkey wheat; *B*, scattered small foot-rot spots in a field of Kanred wheat in which *Ophiobolus graminis, Helminthosporium sativum*, and *Wojnowicia graminis* were present



A.Hoen & Co Baltimore

TAKE-ALL OF GOLDCOIN WHEAT—I

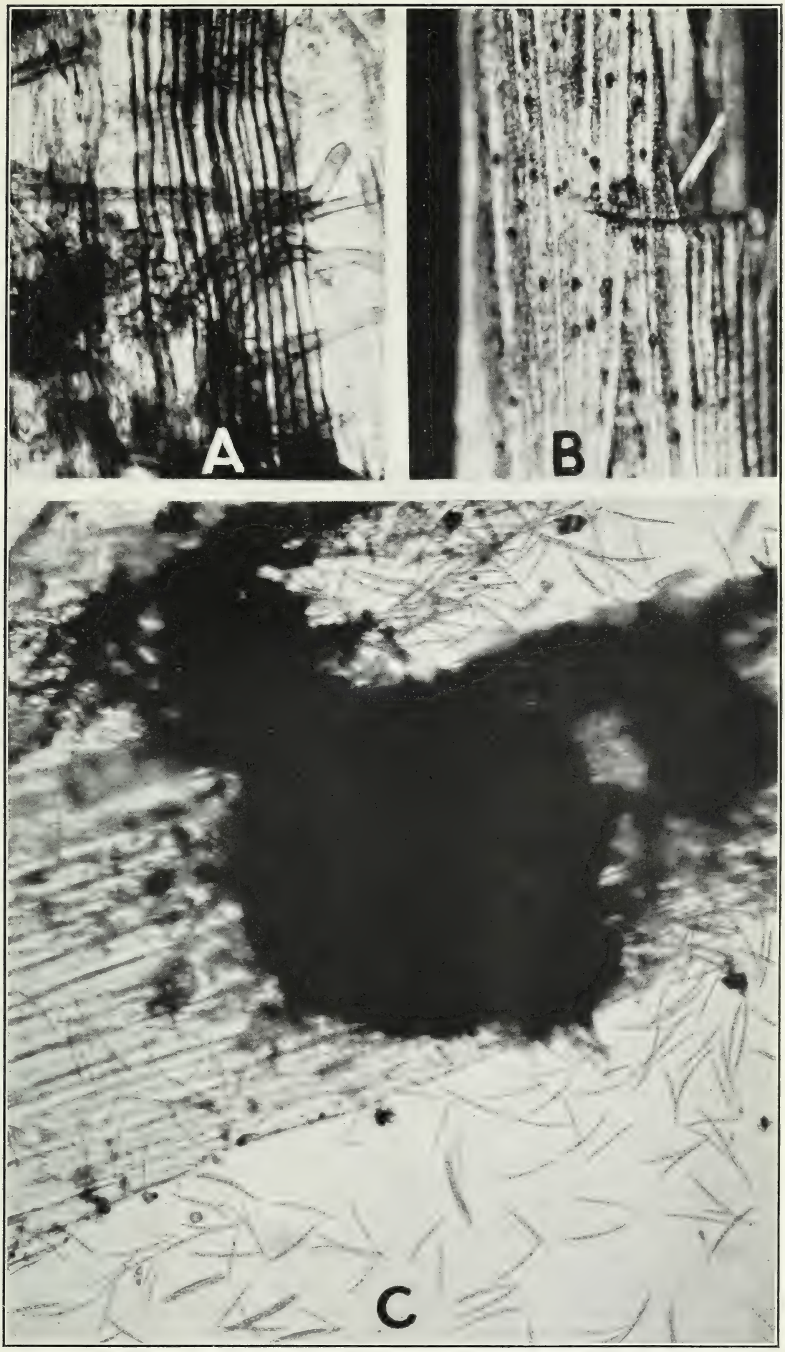
The seedling at the left is healthy, and the five others at the right show various degrees of severity of seedling blight following artificial inoculation with a single-spore strain of *Ophiobolus graminis* isolated from a wheat plant affected with take-all near Corvallis, Oreg. All the roots on the diseased plants were badly rotted. Note the reddish brown to black lesions and rotting at the base of the stems



A. Hoen & Co. Baltimore.

TAKE-ALL OF GOLDCOIN WHEAT—II

A healthy seedling is shown at the right. The three others were killed by *Ophiobolus graminis* under field condition near Corvallis, Oreg., in 1921. Note their blackened bases and stunted, yellowed condition.



OPHIOBOLUS GRAMINIS ON WHEAT

A, Mycelial plate from underground leaf sheath, ×450; *B*, necks of perithecia projecting through basal sheath of wheat plant affected with take-all, ×20; *C*, perithecium on under side of basal wheat leaf sheath and free asci and ascospores, ×135

pathologists over the world continued to designate the take-all fungus *O. graminis.*

Fitzpatrick, Thomas, and Kirby (*21*) inquired into this subject. They concluded that Berlese was in error concerning the identity of *Ophiobolus eucryptus* with *O. cariceti* and *O. graminis* and held that the take-all fungus should be designated *O. cariceti.* In going over the evidence presented by these workers it is found that they were unable to obtain mature ascus-bearing type material of any of the three species under discussion. They did study specimens of *O. eucryptus* on iris, an entirely different host plant from the original, and found the asci and ascospores to be different from those of the take-all fungus they were studying. As to *O. cariceti*, they base their identification of this on material in Cooke's herbarium collected by Broome but clearly not part of the type collection, and it is doubtful whether Broome even identified the fungus on this material, as evidenced by Wakefield's letter published by Fitzpatrick and his collaborators (*21*).

From the evidence presented by Fitzpatrick, Thomas, and Kirby it seems reasonable to believe that no ascus-bearing type specimens of *Ophiobolus eucryptus* and *O. cariceti* are now in existence, but the original descriptions and figures (*5*, *6*) may be taken to represent them. Reference to these descriptions and drawings shows that *O. cariceti* is described with ascospores measuring 0.003 to 0.004 inch (76.2 to 101.6 microns) in length, whereas *O. eucryptus* is described with ascospores measuring 1/500 inch (50.8 microns) in length, thus clearly showing that two distinct species are involved. In view of the wide difference between the spore lengths given in these original descriptions it is difficult to understand the interpretation of Berlese (*7*) that the two species are identical. It is possible that he committed an error when he compared the types of these species, as was pointed out by Fitzpatrick, Thomas, and Kirby, but if he did it seems quite clear that his comparison between the type materials of *O. cariceti* and *O. graminis* should also be looked upon with doubt and certainly should not be considered as a basis for a change in the nomenclature of the take-all fungus, as was done by Fitzpatrick and his collaborators.

It is also possible that Berkeley and Broome described their material inaccurately, but in the absence of the type specimens it is impossible to determine this point, and it therefore seems quite clear that *Ophiobolus eucryptus* and *O. cariceti* can not now be considered identical.

As to the identity of *Ophiobolus graminis* with the other two species under discussion at present it is only possible to compare the published descriptions. A study of the type material of *O. graminis*, which is presumably in existence, might throw some light on the matter, but this seems doubtful, because all of the take-all fungus which has been described by various workers has essentially answered Saccardo's description of *O. graminis.* This fungus is described as having ascospores measuring 70 to 75 microns in length and 3 microns in width. Clearly this length dimension falls between those for *O. eucryptus* and *O. cariceti.* As the exact widths were not recorded for the last mentioned species, this can not be used as a means of comparison.

In comparing the ascospores and perithecia of several strains of Ophiobolus obtained on wheat from various localities in this country with the three original descriptions under consideration, it seems evident that we are dealing with *O. graminis* Sacc. The writer has noted some variations in the size of spores in the several strains of *O. graminis* being studied, but such variations have not tended in the direction of *O. cariceti*, nor have they yet been found to vary to the extent that they reached the length recorded for *O. eucryptus*.

Rather extreme variations in the size and shape of the perithecia of *Ophiobolus graminis* also have been noted by the writer, and it has been found that the frequently smooth pycnidia of *Wojnowicia graminis* (McAlp.) Sacc. and D. Sacc. are in many cases indistinguishable from the perithecia of *O. graminis* both with respect to form and position on the host. Frequently the pycnidia of *W. graminis* and the perithecia of *O. graminis* are found on the same plant, and the pycnidia often occur independently on diseased wheat plants in the areas where *O. graminis* occurs. As yet our own studies have not advanced to the point where we can be certain that we are dealing with *O. graminis* on diseased wheat plants until the contents of mature fruiting bodies have been examined microscopically. The writer knows of no published work giving descriptions or methods which will assist in distinguishing with certainty the perithecia of *O. graminis* from many of the pycnidia of *W. graminis*, and all observations which have been made by him indicate that any attempt to identify *O. graminis* on a basis of the perithecia, as suggested by Fitzpatrick, Thomas, and Kirby (*21*), is likely to lead to error.

As the problem of nomenclature of the take-all fungus now stands, it appears that ascus-bearing type material of *Ophiobolus eucryptus* and *O. cariceti* is no longer in existence, and therefore the original descriptions and drawings of these species are our only means of identification. On the basis of these descriptions and on that of Saccardo for *O. graminis* it is only reasonable to consider that all three species are distinct, and as the Ophiobolus, which the writer and many other workers, including Fitzpatrick, Thomas, and Kirby (*21*), have found to cause the take-all disease essentially conforms to Saccardo's description, the writer will continue to designate it by the widely accepted name *Ophiobolus graminis* Sacc.

Ophiobolus graminis was considered the cause of a foot-rot in Europe and take-all in Australia for a number of years before the experimental proof was presented. Mangin (*50*) and Delacroix (*17*), working in France, carried out inoculation experiments which indicated rather clearly that this organism causes the disease in question. In these experiments these workers obtained ascospores of the fungus from perithecia produced on diseased plants. They prepared water suspensions of these ascospores and applied them to soil in which wheat plants were growing. In the case of Mangin's experiments infection was somewhat delayed, but after replanting in the inoculated soil he obtained the disease. Delacroix found, more readily than did Mangin, that *O. graminis* produced typical foot-rot (take-all) symptoms. Plants growing under the same conditions but in uninoculated soils remained healthy. While all the plants growing in Delacroix's inoculated soil did not become infected, those which did showed the typical symptoms of take-all.

Waters (*73*), working in New Zealand, demonstrated the pathogenicity of the fungus by applying pure-culture material to wheat plants growing in tubes of sterilized soil. Kirby (*37*) and Davis, working in this country, have found *O. graminis* pathogenic on wheat and capable of producing the symptoms of take-all.

HOST RANGE OF OPHIOBOLUS GRAMINIS

In Australia (*42*), New Zealand (*72*), Japan, (*31*), and France (*25*) this parasite attacks wheat, rye, and barley. McAlpine (*41*) states that in Australia the fungus occurs on *Bromus sterilis*, an introduced grass, and Darnell-Smith and MacKinnon (*16*, *pp. 25–27*) say that the fungus also occurs on *Hordeum murinum*. According to Waters (*72*), in New Zealand the fungus has been found to attack *H. murinum*, *B. sterilis*, and *Agropyron repens*. In Japan Hori (*31*) reports that the organism also parasitizes wet-land rice. In England the fungus has been reported frequently on wheat and oats, and it has been found on oats in Australia, but from the literature and from observations made in America it is evident that oats are not seriously injured by this parasite. In fact, Sutton (*68*) claims that under Australian conditions oats are practically immune from the attack of this fungus and that this crop assumes an important place in rotations on soils infested with the parasite.

In America *Ophiobolus graminis* has been found to occur naturally on wheat, rye (*37*), *Agropyron repens* (*37*), *Bromus secalinus* (*61*), *Chaetochloa geniculata* (*61*), *Festuca octoflora* (*61*), *F. elatior* (*61*), and *Hordeum pusillum* (*61*). Kirby (*37*) has artificially inoculated several wild grasses growing under greenhouse conditions and found that a number of species are susceptible to Ophiobolus infection. Of the 48 grasses studied just half the species were susceptible. Six common species of Agropyron were inoculated, and all became infected. According to Kirby's data *A. repens* developed the most severe infection of all the wild grasses inoculated. On the whole, these inoculation tests indicate that many of our most widely distributed wild grasses may play an important part in carrying *O. graminis* from one season to another, thus materially complicating any control program.

LIFE HISTORY OF OPHIOBOLUS GRAMINIS

As pointed out by Lindau (*40*) and Kirby (*37*), the complete life cycle of this parasite is not known with certainty. Several workers claim to have found a conidial stage, but this has never been proved definitely. Mangin (*50*) thought the conidial stage to be *Coniosporium rhizophilum*, but his evidence was based on the mere association between the latter form and *Ophiobolus graminis* on diseased wheat plants. McAlpine (*41*) found an undescribed pycnidial form associated with *O. graminis* which he says appeared to be the pycnidial stage of the latter organism. McAlpine described the pycnidial form and named it *Hendersonia graminis* n. sp. Subsequently Saccardo and D. Saccardo transferred the species to the genus Wojnowicia, and thus the name became *Wojnowicia graminis* (McAlp.) Sacc. and D. Sacc. This fungus has been found associated with *O. graminis* in this country, but, as pointed out by McKinney and Johnson (*47*), the cultural behavior of these two forms is sufficiently different to cause one to doubt any genetic connection between them.

Kirby (*37*) reports that the ascospores of *Ophiobolus graminis* live through the winter in the soil. Davis[8] confirms this. He also found that the mycelium survives the winter. Many workers seem to consider that *O. graminis* infects chiefly, if not entirely, by means of its ascospores, but no doubt the mycelium is of importance also, especially as several workers (*37*, *73*) have shown that the fungus mycelium can live saprophytically for a time at least and that the mycelium is infectious. Further data are needed on the relative importance of ascospores and mycelium as infective agents. Information is also lacking on the relative importance of ascospores and mycelium as hold-over infective materials. It seems well to consider the possible importance of the vegetative stage of the fungus under field conditions. General field observations indicate that the fungus can not exist long as a saprophyte, but experimental evidence on this point is lacking.

The writer has noted some irregularity in the habits of this fungus with regard to the production of fruiting bodies. This has been especially noticeable in the take-all experimental plats located at Abilene, Kans., and on the agronomy plats located on the experiment station farm at Manhattan, Kans. During the past four years the symptoms of take-all have developed in a more or less typical way at Abilene, but not until 1923 did the writer find the mature perithecia of the fungus, and then the fruiting bodies were very scarce and difficult to find. Doubtless perithecia had developed previously, but they were not found. In Oregon it has been noted that the fruiting bodies of the fungus do not develop as frequently in some years as in others. The writer examined take-all plants collected near Corvallis, Oreg., in 1921, and found that perithecia were very sparse. In 1923 take-all plants were collected by H. Fellows in a field adjacent to the one observed in 1921, and fruiting bodies were found to be exceedingly abundant. These observations are borne out in a measure by McAlpine (*41*), who states that "In dry seasons and during certain periods of the year only the vegetative portion of the fungus may be found * * *." If perithecial development is influenced by seasonal factors it probably is also affected by climatic differences in different localities. Take-all material collected in North Carolina and New York shows an abundance of fruiting bodies on a large proportion of the diseased stalks.

Kirby (*38*) has stated that *Ophiobolus graminis* is heterothallic, which, if true, would explain some of the irregularities cited in connection with the production of perithecia. However, the studies by Davis indicate that more evidence must be presented before the occurrence of heterothallism in *O. graminis* is fully established. In certain strains of this fungus Davis has shown clearly that heterothallism does not exist.

FACTORS INFLUENCING THE DEVELOPMENT OF TAKE-ALL

Many statements are found in foreign literature regarding the influence of weather and seasonal conditions on the foot-rots and take-all. In nearly all cases conclusions have been based on rather casual observations, which in many instances have been made with regard to foot-rots in general rather than a specific foot-rot. Obviously, many uncontrollable factors enter into field observations which make it very difficult or impossible to interpret properly the exact influence of seasonal and climatic factors, and it becomes necessary to carry out experiments in which the conditions can be controlled to a greater degree than is possible in the field. Such experiments dealing with the influence of temperature and soil moisture have been carried out by R. J. Davis and the writer, and the results will be published in another paper.[9] In general, these results show that fairly low soil temperatures (12° to 16° C.) are most favorable for the infection and injury of seedlings and young wheat plants. They also indicate that take-all is more severe when the soil is too wet or too dry for the best development of the wheat plant. However, wet soil seems to be more favorable for the disease than dry soil. The general summary of the results obtained in temperature studies is represented by the curve shown in Figure 2. Other phases of the take-all disease must be studied before it will be possible to analyze thoroughly the temperature and soil-moisture data now in hand, and these latter factors also need further study. As pointed out earlier in this bulletin, *Ophiobolus graminis* behaves in a very perplexing way at times in regard to both fruiting and infection; and, aside from apparent differences in strains of the fungus, it seems probable that environmental factors may be playing an important rôle in bringing about some of these irregularities.

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[8] Davis, R. J. Studies on Ophiobolus graminis Sacc. and the Take-All Disease of Wheat. (Unpublished manuscript.)

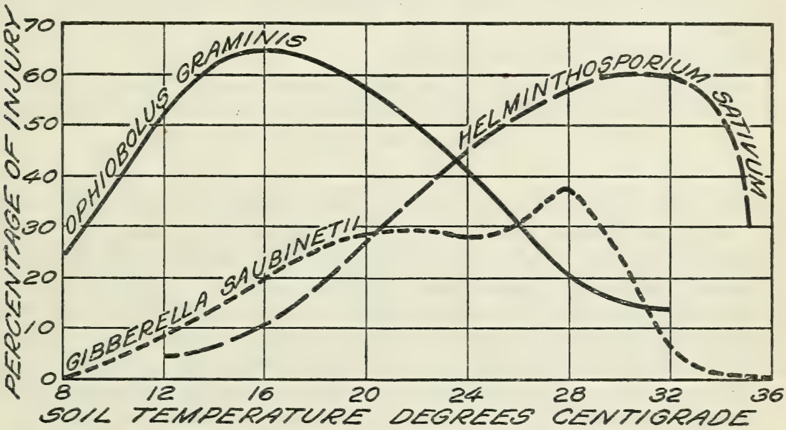

FIG. 2.—Curves representing the influence of soil temperature on the infection and injury of seedlings and young plants of winter wheat when grown in experimental soils infested with pure cultures of *Ophiobolus graminis, Helminthosporium sativum* (*45*), and *Gibberella saubinetii* (*18*). As these curves are based on experiments conducted under somewhat different conditions and as the data were not all obtained in exactly the same manner the curves do not express with complete exactness the relative infective powers of the three parasites

The exact influences of soil type and fertility on the development of take-all are not definitely known, but it seems evident from the reports of foreign workers and from observations made in this country that there are other factors which exert greater influence on the development of the disease than these. Hori (*31*) states that the disease seems to be more prevalent in Japan on clay, clay loam, and gritty clay land, and he has found the disease less prevalent on sandy soil. McAlpine (*41*) and Sutton (*68*) in Australia find that the disease occurs on all kinds of soils and in all locations. It is stated also that take-all is serious on the best soils. In this country take-all is not restricted to any particular soil type or to soils showing any particular degree of fertility. The writer has observed fields in Kansas, Oregon, and New York where the disease occurred on the best of soil. However, in other localities, as in Knox County, Ind., and in Arkansas, the disease appeared on soils poor in texture and fertility. Rosen and Elliott (*61*) reported that take-all was associated primarily with poor infertile soils. This is true for the known locations of take-all in Arkansas, but more extensive observations in other parts of the country show distinctly that this correlation does not always exist.

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[9] McKinney, H. H., and Davis, R. J. The Influence of Soil Temperature and Moisture on Infection of Wheat Seedlings by Ophiobolus graminis. (Unpublished manuscript.)

The effects of fertilizers and amendments and tillage methods on take-all will be considered later in connection with control measures.

CONTROL OF TAKE-ALL

It has been pointed out elsewhere in this bulletin that there is no evidence that *Ophiobolus graminis* infects the heads or seed of plants, and therefore seed-treatment methods have little bearing on the control of take-all. However, as bits of straw bearing the perithecia and mycelium of the fungus may get into the grain at threshing time, care must be exercised in connection with the use of seed from fields infested with take-all. Such seed should be very thoroughly cleaned before sowing, in order to prevent the introduction of the fungus into the soil through the seed, or, better still, avoided entirely.

Take-all is caused by a soil-borne parasite; hence the problem of its control becomes immediately centered on the soil and on cropping methods. As in the case of observations dealing with the influence of seasonal conditions on the development of the disease, many of the control measures which have been recommended have had to do with more than one foot-rot or with a foot-rot of uncertain cause. In most cases field experiments dealing with soil treatments and cropping and tillage systems have been carried out in plats which were not uniformly infested with the parasite, and in other cases the experiments have not been conducted over sufficiently long periods to enable the drawing of reliable conclusions. The writer's experience with take-all in this country indicates that it is rather difficult to find uniformly infested areas which are sufficiently large for plat treatment and cropping experiments, and no doubt foreign workers have encountered the same difficulty. This condition makes it necessary to use relatively small plats of uniformly infested soil in conjunction with larger field plats, and in addition it is essential that experiments be carried on over a period of years before arriving at definite conclusions.

The control influence of various fertilizers has been studied by several workers, but there is not full agreement as to the influence of these treatments on the disease. Reuther (*60*) claims that excessive nitrogen favors take-all and other foot-rots, but he thinks that fertilizers containing potassium tend to reduce their severity. Hori (*31*) states that take-all is most severe when applications of nitrogenous fertilizers have been made and when the three essential elements are unbalanced. Other investigators claim that nitrogenous fertilizers intensify foot-rot; still others, that they tend to control it. It is not clear in all cases, however, that these investigators are dealing with *Ophiobolus graminis.* Rosen and Elliott (*61*) report that during the one year their experiments were conducted the amount of take-all was greatly reduced by the use of a complete wheat fertilizer and farm manure.

In general, it seems that the phosphate fertilizers, such as acid phosphate, Thomas phosphate, and superphosphate of lime, tend to reduce take-all, whereas nitrogenous fertilizers tend to increase the severity of the disease. While further studies must be made before the exact influences of these fertilizers on take-all will be known, it would seem apparent from results now in hand that the success of these materials is tied up with some other influencing factor or set of factors.

There are several statements in the literature cited concerning the effect of lime on the development of take-all, but, as Brittlebank (*11*) points out, it is not definitely known whether the disease is favored by an acid or an alkaline soil. In some of Brittlebank's field experiments he found that applications of lime to the soil increased the infestation of take-all, but he was not inclined to draw definite conclusions from these experiments on account of their short duration. Kirby (*37*) studied the influence of various hydrogen-ion concentrations on the growth of *Ophiobolus graminis* in pure culture and reported that alkaline media were most favorable. He also carried on pot experiments in which he made applications of lime and sulphur. Although these were rather limited, Kirby concluded that lime favors development of the disease.

Davis made preliminary studies on the growth of several strains of *Ophiobolus graminis* on artificial media varying in hydrogen-ion concentrations, and his results indicate that growth is favored by a slightly acid substrate. Kirby and Davis did not follow exactly the same methods, in that Kirby's cultures were grown in the dark and those of Davis in the light. Also, Davis's cultures were grown for a longer period. Webb and Fellows[10] took up this problem in a rather comprehensive manner in order that the seeming discrepancies in the results of Kirby and Davis might be harmonized if possible. Their results indicate that the type of medium used and the method employed in its preparation have much to do with the influence of the hydrogen-ion concentration on the growth of the fungus. They have shown that under certain conditions the fungus is favored by an acid medium, whereas under another set of conditions growth is favored by an alkaline substrate. It appears that the fungus thrives over a rather wide range of acid and alkaline reactions when grown in certain media. This relationship makes it appear that the control of take-all through attempts to adjust soil reactions is likely to be very uncertain.

Such disinfectants as copper sulphate, corrosive sublimate, lime-sulphur, and sulphuric acid have been applied to infested soil with varying degrees of success in controlling the disease. Even when successful, however, the expense of these disinfectants in many cases is considerable, and under the present conditions these methods are not recommended for extensive application in the field. Ferrous sulphate has been used with a considerable degree of success in Australia. It is claimed that when this chemical is applied to the soil at rates varying between 50 and 75 pounds per acre, the amount of take-all is materially reduced.

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[10] Webb, R. W., and Fellows, H. Growth of Ophiobolus graminis Sacc. in Relation to Hydrogen-ion Concentration. (Unpublished manuscript.)

Numerous cropping systems and methods of tillage have been proposed to combat take-all, but it appears that the details of such methods must be worked out for the particular climatic conditions confronting the grower. The bulk of evidence available indicates that summer fallowing and clean cultivation of infested land tend to reduce take-all in the following wheat crop. It also is generally accepted that oats are a safe crop for rotation on infested soil. Take-all is not known to occur on maize or any of the sorghums or legumes, and it seems apparent that these are safe rotation crops, in spite of the claim of certain European investigators that legumes facilitate the growth of the fungus in the soil. Owing to the many grasses attacked by *Ophiobolus graminis*, take-all can not be eradicated by allowing infested land to lie in pasture. The burning of infested stubble immediately after harvest is recommended widely in Australia and is considered one of the best means of reducing infestation. When this practice is followed the stubble is usually left as long as possible or the wheat is not cut at all. The stubble is then rolled and burned.

Late fall sowing has been recommended by several foreign workers as a means of reducing take-all, but owing to the many uncertain factors entering into this practice this method should not be recommended too strongly in the United States until more is known about the influences of environmental factors on infection.

Several European workers state that heavy seeding tends to increase the severity of the disease, and they have recommended light seeding on infested soils. However, preliminary experiments carried out in this country have not given results which permit a definite statement on this point.

The use of resistant varieties has been recommended by several workers, but as far as can be determined from the literature no variety of wheat has been found which consistently shows outstanding resistance to take-all. Pridham (*56*) tested a considerable number of varieties of wheat under Australian field conditions and found several which were not attacked so severely by *Ophiobolus graminis* as were many others. He noted that early short-season varieties were damaged less by the disease than were the late long-season ones. These experiments were carried on for only a year, however, and it is not known whether the variations shown among the wheats were largely varietal in nature or due in part to other variables. McAlpine (*41*) points out that on some farms Dart's Imperial wheat is comparatively free from take-all, whereas on other farms this variety is severely attacked. The same irregularity is said to occur with the variety known as Queen's Jubilee. Kirby (*37*), working under greenhouse conditions, reports that the wheat varieties he tested showed but slight differences in susceptibility to take-all. Several workers report that introduced or nonacclimated varieties are more susceptible to take-all than are local ones. It is also stated by others that early varieties and red wheats are more subject to take-all than are the late sorts and the light-colored varieties.

Although the work being carried on by the United States Department of Agriculture and the cooperating State experiment stations has not progressed far enough to warrant the publication of definite control measures based entirely thereon, it seems evident that certain measures can be safely recommended. They are as follows:

(1) If possible, avoid the use of seed from take-all infested fields. If absolutely necessary to use such seed, it should be cleaned very thoroughly and given a standard seed treatment.

(2) Avoid the continuous cropping of take-all infested land with wheat, barley, rye, or any of the other grass crops which may be severely attacked by *Ophiobolus graminis*.

(3) Use nitrogenous fertilizers with caution.

(4) Rotate with oats, root crops, or other crops which are known to be immune from the attacks of the parasite. None of the maize or sorghum species or the legumes have yet been found to be attacked by *Ophiobolus graminis*.

(5) In localities where summer fallowing is practiced, this method of control may be advantageous. Fallowed land should be kept free from wild or weed grasses. When practicable, such fallowed land should be cropped at least one year with a nonsusceptible crop, such as oats, corn, the sorghums, or a legume, before wheat is again sown.

THE FOOT-ROT CAUSED BY HELMINTHOSPORIUM SATIVUM

COMMON NAMES

Root-rot, America. Bolley (*10*).
Foot-rot, America. Stevens (*66*).
Helminthosporium blight, America. Weniger (*74*).
Helminthosporium disease, America. McKinney (*43*).

Because the parasite causing the Helminthosporium disease attacks all parts of the wheat plant, several names have been applied to describe the various symptoms produced. However, as this bulletin deals primarily with the foot-rot phase, the other types of injury will be taken up only incidentally.

GEOGRAPHIC DISTRIBUTION

Mangin (*51*) in France, Palm (*52*) in Java, Pridham (*55*), Waterhouse (*71*), and Hamblin (*26*) in Australia, and Butler (*12*) in India have found species of Helminthosporium associated with diseased wheat, but in most cases the exact species involved are questionable or unknown. Butler (*12*) states that in India wheat is attacked by several species or forms of Helminthosporium. Drechsler (*19*) in his bibliographical treatment of the Helminthosporium diseases of certain grasses concludes on a basis of the literature that Palm and Hamblin were working with *Helminthosporium sativum*. Christensen (*13*) states in this connection that he has seen Hamblin's organism and that it is *H. sativum*. Christensen says, further, that he also has obtained cultures of *H. sativum* from Canada, Mexico, and Argentina, and he concludes that the disease is prevalent in these countries.

In this country severe Helminthosporium attacks on wheat were first reported by Beckwith (*4*) and Bolley (*9, 10*) in North Dakota.

Since these reports, many more have been made from other States, and it is evident, as stated by the writer in previous publications (*43*, *44*), that the Helminthosporium foot-rot of wheat is seemingly widespread throughout the winter and spring wheat districts. The distribution of the disease is shown in Table 2 and Figure 3, and comparisons with Table 1 and Figure 1, respectively, will show that in America this disease is more widespread than take-all.

TABLE 2.—*Distribution of wheat foot-rot caused by Helminthosporium sativum in the United States*

[The sources of information for certain items are indicated as follows: *Reports of the Office of Plant Disease Survey, U. S. Department of Agriculture; †correspondence of the Office of Cereal Investigations, U. S. Department of Agriculture; ‡J. J. Christensen (*13*); §Mrs. L. J. Stakman (*65*)]

Year	State and county	Collector	Organism identified by—
	Colorado:		
*†1919	Arapahoe	J. G. Leach	J. G. Leach and the writer.
	Idaho:		
1921	Fremont	County agent	The writer.
	Illinois:		
1919–1923	Madison	The writer and several other workers.	The writer and several other workers.
1919	Mason	do	Do.
1919	Sangamon	do	Do.
1919–1923	Logan	do	Do.
1920	Champaign	do	Do.
	Indiana:		
1919–1923	LaPorte	do	Do.
1919	Porter	do	Do.
1919	Tippecanoe	do	Do.
‡	Iowa		J. J. Christensen.
	Kansas:		
1920–1923	Dickinson	L. E. Melchers and the writer	The writer.
1922	Douglas	The writer	Do.
1921	Leavenworth	L. E. Melchers and the writer	Do.
1921	Jefferson	do	Do.
1923	Riley	The writer	Do.
	Minnesota:		
§1918	Ramsey		Mrs. L. J. Stakman.
‡1919	Sherburne		J. J. Christensen.
1920	St. Louis	H. D. Barker	The writer.
‡1921	do		J. J. Christensen.
1921	Hennepin	The writer	The writer.
‡1921	Anoka		J. J. Christensen.
‡1921	Kittson		Do.
‡1921	Pennington		Do.
‡1921	Marshall		Do.
‡1921	Wilkin		Do.
‡1922	Dakota		Do.
‡1922	McLeod		Do.
‡1922	Rice		Do.
‡1922	Renville		Do.
‡1922	Meeker		Do.
‡1922	Chippewa		Do.
‡1922	Polk		Do.
‡1922	Scott		Do.
‡	Nebraska		Do.
	Missouri:		
1919	St. Louis	The writer	The writer.
‡	New Mexico		J. J. Christensen.
*1921	New York	R. S. Kirby	R. S. Kirby.
	North Dakota:		
*Every year	Wheat-growing counties.	Numerous collectors	Several workers, including the writer.
	Oklahoma:		
1923	Woodward	L. F. Locke	The writer.
	South Dakota:		
1921	Brown	A. T. Evans	Do.
‡	Texas		J. J. Christensen.
	Washington:		
1919	Thurston	F. D. Heald and the writer	The writer.
‡	West Virginia		J. J. Christensen.
	Wisconsin:		
1920–21	Fond du Lac	J. G. Dickson and the writer	Helen Johann and the writer.
1919–1923	Dane	The writer and others	The writer.

ECONOMIC IMPORTANCE

According to Stakman (*65*) this Helminthosporium foot-rot caused as high as 50 per cent damage in wheat fields in certain districts in Minnesota during 1919. She states that in the previous year some of the experimental wheat plats on the university farm had to be discarded on account of the disease. Christensen (*13*) states that the disease was reported from practically every important wheat-growing county in Minnesota in 1919 and that in some localities it caused considerable losses. He states further that in certain cases fields of wheat were so badly injured that they were plowed and planted to corn, and that in 1921 and 1922 the disease was very severe and widespread in wheat, rye, and barley, 10 to 20 per cent losses occurring in barley and wheat fields in 1922. Christensen also states that *H. sativum* appears to cause most of the root rotting of wheat, barley, and rye in Minnesota.

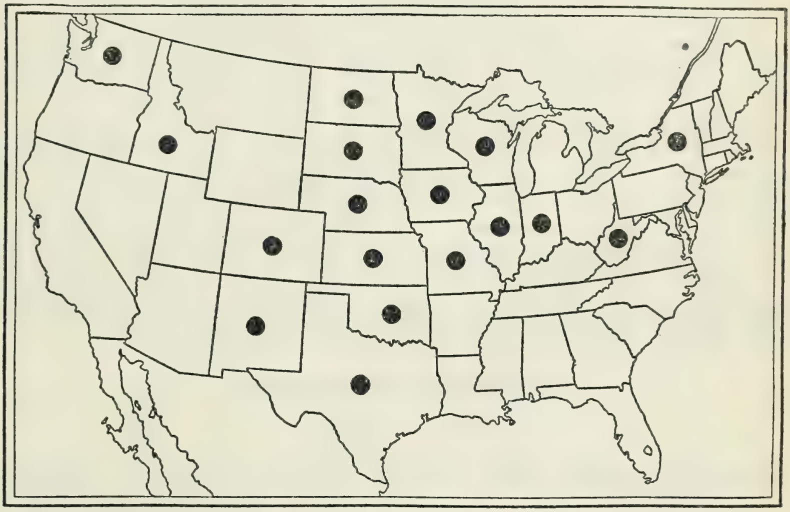

FIG. 3.—Outline map of the United States, showing by means of dots the States in which the wheat foot-rot caused by *Helminthosporium sativum* has been found

Weniger (*74*) states that in North Dakota as high as 70 per cent of the wheat plants in a field may be attacked by *Helminthosporium* sp.[11] She says that for a number of years this disease has caused great losses, especially in the durum wheats in the eastern part of North Dakota, and that the seedling blight caused by this fungus is as severe as that caused by *Fusarium* sp. Bolley (*10*) has indicated that *Helminthosporium* sp. is the most common parasite attacking the underground parts of wheat plants in North Dakota.

Raeder (*58*), working in Idaho, reports a Helminthosporium on wheat in several counties, and according to Haskell and Wood (*27*) Richards reports that a Helminthosporium is associated with a root-rot of wheat in Utah. In 1921 the writer made plating studies of a considerable quantity of diseased wheat material from Fremont County, Idaho. *Helminthosporium sativum* was obtained in most cases. The symptoms manifested by these diseased wheat plants answered the description given by Raeder (*58*), and they were indistinguishable from the symptoms produced by *H. sativum* in the central wheat regions.

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[11] The writer has collected numerous specimens of similarly infected wheat plants from fields in North Dakota, and in the cases where Helminthosporium appeared it was always found to be *H. sativum.*

During the past five seasons the writer has made many field observations in different parts of the winter-wheat regions and has made many culture platings from the diseased wheat plants collected by him and by others. In many cases *Helminthosporium sativum* has been found associated with other parasites, and it has been difficult and often impossible to determine just how much of the crop damage could be attributed to *H. sativum.* This is especially the case in certain parts of Kansas where *Ophiobolus graminis*, *Wojnowicia graminis*, *H. sativum*, and several species of Fusarium occur together and in parts of Wisconsin where *H. sativum* is associated with *Gibberella saubinetii.* On a basis of the literature and from the writer's observations it appears that *H. sativum* does not cause such heavy losses in the winter-wheat belt as it seems to cause in the spring-wheat belt. Severe seedling infection or seedling blight of winter wheat, amounting to economic importance, has never been noted by the writer. Severe infection of the outer leaf sheaths of seedlings frequently occurs, especially in early-sown fall wheat (*44*, *45*), but it appears that this infection seldom injures the plant as a whole. Root lesions have never been found abundantly on fall-wheat plants, and such lesions have never been noted to occur extensively during the spring and summer growing periods.

DESCRIPTION OF THE DISEASE

FIELD APPEARANCE

The field spotting which several workers (*13*, *26*, *65*) report as caused by *Helminthosporium sativum* does not seem to be produced in all localities where the parasite occurs. This spotting seems to be prevalent in the spring-wheat region, but the writer has never noted in winter wheat a field spotting which was certainly caused by *H. sativum.* A spotting in wheat fields has been reported to the writer several times from the vicinity of Woodward, Okla., and while *H. sativum* has been found on many of the diseased plants sent to him, other fungi have been found, and these may play a part in causing field spots. On the other hand, it seems probable that *H. sativum* will produce more severe injury to winter wheat when grown in the more southern regions, which have rather long and relatively warm fall periods. Consequently, it would not be surprising to find this parasite causing a definite field spotting in such localities.

The rosette disease (*44*) occurring in certain varieties of winter wheat in Illinois and Indiana causes a field spotting, and in some cases *Helminthosporium sativum* is associated with this disease; but, as pointed out later, carefully conducted experiments have shown that wheat rosette is not caused by *H. sativum* (*49*).

DISEASE SYMPTOMS

Although wheat seedlings are frequently killed by *Helminthosporium sativum*, this condition has not been observed to any extent in the winter-wheat regions. Under conditions favorable for the fungus it causes a rotting of the roots. In less severe cases dark-brown lesions develop on the roots at points of infection, causing but little apparent injury to the plant. The coleoptile, basal leaf sheath, and stem may show various degrees of infection from small elongated lesions to a complete rotting. In severe cases of root or stem rot the seedling leaves show a dark-green coloration or sometimes a chlorosis, and later the whole seedling usually dies. In the case of older plants the type of root and culm injury is much the same as that occurring on seedlings, except that there seems to be less tendency for a complete rotting of the stem.

The fungus attacks the leaf blades, sheaths, upper culm, and head. The kernels also become infected and develop a dark-brown to black tip at the germ end. This condition has been called blackpoint by Bolley (*10*), Evans (*20*), Weniger (*74*), and Henry (*30*). So far as known no part of the wheat plant is immune to infection from this parasite at any period during its development. Stem and foliage lesions tend to be elliptical in outline. Usually these consist of a dark-brown margin with a lighter brown center, as illustrated previously (*45*). On leaves these centers frequently drop out, and in some cases lesions may involve the entire width of the leaf. This fungus also produces a spot blotch on the leaves of barley plants, but on this host the spots tend to be uniformly dark brown or almost black in color. They do not incline to the light centers which characterize the leaf spots produced on wheat leaves.

On the roots and stems of wheat seedlings *Helminthosporium sativum* causes the tissues to develop a light to chocolate brown coloration. This color is usually darker than that produced by *Gibberella saubinetii*, and there is no suggestion of pink or red, such as that which is frequently associated with the attacks by the last-mentioned parasite. In some cases, however, the light-brown coloration and rotting produced by these two parasites are so similar that they can not be distinguished by ordinary means of superficial examination.

Occasionally observations have shown that *Helminthosporium sativum* produces a black coloration on the roots and bases of stems which may be readily confused with the blackening produced by the mycelial plate of *Ophiobolus graminis* unless the specimens are examined very carefully. Microscopic observations on such plants show that this blackening may be produced in at least two ways. The dark brown to black conidia may develop in a crust on the infected parts or the host cells of the infected tissues may contain very dark brown to black amorphous masses seemingly of a reactionary nature. In some cases the cortical cells of the roots thus affected slough away and become loosely attached to the roots, thus producing an effect resembling a mycelial plate when examined macroscopically.

The blackening caused by masses of conidia has been noted a very few times under field conditions, but it has never been obtained on greenhouse-grown plants. The second type of blackening has been obtained in experimental material and then only occasionally when large amounts of inoculum were used. The writer has not observed this type of blackening in nature, though there seems to be no reason why it would not occur if the proper conditions were obtained. He has never found *Helminthosporium sativum* producing a mycelial crust or plate in any way similar to that produced by *Ophiobolus graminis.* Weniger (*74*) reports that a black coloration is sometimes associated with Helminthosporium foot-rot in spring wheat in North Dakota, but she does not state the exact nature of this coloration.

Christensen (*13*) states that spring wheats and barley may show excessive tillering and become stunted when infected by *Helminthosporium sativum.* In this regard there seems to be a similarity to the rosette disease (*44*) occurring in certain varieties of winter wheat. Although the writer (*44*) has mentioned that certain spring wheats and barleys infected by this parasite develop symptoms similar to rosette, he has never noted that these crops develop the same degree of tillering or certain of the other symptoms which occur in winter wheats affected by rosette. Data have been published (*44*) which indicate that *H. sativum* will increase tillering in Harvest Queen (winter) wheat, but this condition was not associated with any abnormal appearance of the aboveground portions of the plants.

Stevens (*66*, *67*) has stated that the rosette disease (called foot-rot by him) occurring in winter wheat is caused by *Helminthosporium sativum*, but it has been pointed out several times by the writer (*43*, *44*, *45*) that this causal relationship has not been demonstrated. Evidence (*49*) now in hand indicates that *H. sativum* is not the primary causal agent for the rosette disease.

Several field inoculation experiments carried out by R. W. Webb and the writer with pure cultures of *Helminthosporium sativum* have failed to produce symptoms of the rosette disease in Harvest Queen wheat, a variety which is highly susceptible to rosette. In these experiments a culture of *H. sativum* was used kindly supplied by F. L. Stevens. This culture was isolated by him from a wheat plant affected by the rosette disease and the Helminthosporium foot-rot. Other cultures of *H. sativum* isolated by Webb and the writer also were used in these inoculations. In addition, field soil of long-standing infestation with *H. sativum* was kindly supplied to the writer by J. J. Christensen, of the Minnesota Agricultural Experiment Station, and this soil also failed to produce any suggestion of the rosette disease on Harvest Queen wheat. Experiments carried on at the same time and under the same conditions with soil naturally infested with the rosette causal agent invariably developed a high percentage of rosette.[12]

CAUSE OF THE DISEASE

As pointed out recently by Drechsler (*19*) and by the writer (*45*), Johnson (*35*) appears to be the first to show that *Helminthosporium sativum* is pathogenic on wheat plants. Several other workers (*13*, *43*, *44*, *65*, *66*) also have carried out inoculation tests with this organism and concluded that it is pathogenic on wheat. In the present study the writer found that single-spore strains of *H. sativum* isolated from diseased barley and wheat plants readily reinfected these hosts when cross inoculations were made. Both strains produced the characteristic symptoms on the leaves and subterranean parts of both hosts, and when these strains were reisolated they produced the same symptoms on the reinoculated hosts. This procedure has been carried out repeatedly in sterilized and unsterilized soil to which no artificial medium of any kind was added, and there can be no doubt that the organism in question is parasitic on wheat and barley and that at least certain of the strains of the fungus attack one host as readily as the other.

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[12] Experimental evidence received after this bulletin was prepared for the printer indicates that the rosette disease is a severe expression of a transmissible mosaic, the virus of which persists in certain types of soil for several years. See McKinney, H. H., A mosaic disease of winter wheat and winter rye. U. S. Dept. Agr. Bul. 1361, 10 pp., illus., 1925.

There can be little question that the organism studied by the writer is the same species described by Pammel, King, and Bakke (*53*), occurring on barley leaves. Although several investigators (*13*, *19*, *45*, *67*) have pointed out that this fungus manifests considerable variation in morphology, especially in regard to the conidia (fig. 4, *A* and *B*) when grown on artificial media, the writer has found that conidia produced on leaf lesions of growing barley and wheat plants are more nearly like those of *Helminthosporium sativum* than of any other described species of Helminthosporium.

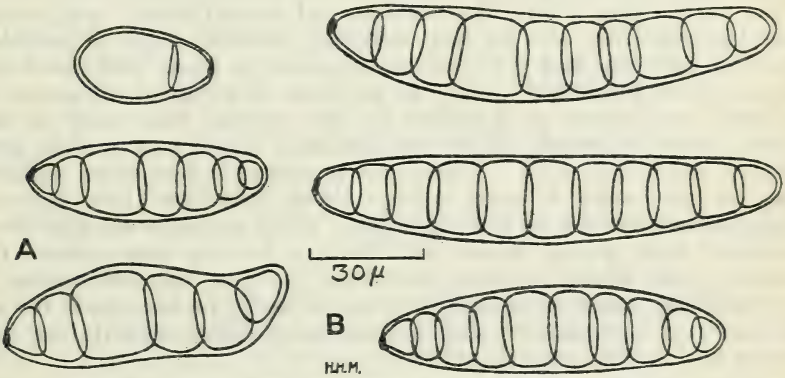

FIG. 4.—Conidia of *Helminthosporium sativum* P., K., and B.: *A*, Grown on potato-glucose agar; *B*, produced on a wheat plant. Type B has also been found on fragments of straw in the soil. This type conforms to the original description for *H. sativum*

HOST RANGE OF HELMINTHOSPORIUM SATIVUM

From the work of Stakman (*65*) and Christensen (*13*) it is evident that this parasite may attack many varieties of wheat, barley, rye, and a good many species of wild grasses. Out of the 113 species and varieties of wild grasses inoculated by Christensen, only 30 gave negative results. None of the three species of Agrostis or the seven species of Poa inoculated was found susceptible to infection.

The writer has not attempted studies dealing with host range, although several varieties of winter and spring wheats have been tested. The results, given in Table 3, were obtained in the greenhouse with sterilized soil which was inoculated just before sowing the wheat seed. Inoculation was accomplished by adding straw cultures of the organism to the soil, which was then thoroughly mixed to obtain uniformity. Three weeks after sowing, all seedlings and unsprouted seeds were removed from the soil and data taken on infection. There was no indication that any seedlings had been killed by the fungus, and no blighting had taken place on any of the plants. In all cases seed germination was about 95 per cent.

TABLE 3.—*Infection in certain varieties of wheat seedlings grown in soil inoculated with a pure culture of Helminthosporium sativum*

[Data based on the degree of injury to the underground portion of the stem and on the number of plants infected]

Variety	Number of plants	Percentage of infection	Variety	Number of plants	Percentage of infection
Marquis	146	90.1	Harvest Queen	188	59.0
Dawson Golden Chaff	109	77.0	Red May	173	55.0
Turkey (Wis. Ped. No. 2)	181	67.2	Illini Chief	147	52.5
Red Wave	156	66.4			

The writer has sown a few varieties of spring wheat and barley near Granite City, Ill., on soil naturally infested with *Helminthosporium sativum*, and portions of the data on these varieties have already been published (*44*). In general, Marquis wheat seems to be more susceptible to infection by *H. sativum* than any of the winter varieties tested. This is shown in Table 3 and in data previously published (*45*). These last-mentioned data also indicate that Hanna barley is more susceptible to infection than Harvest Queen wheat but less so than Marquis. Field experiments also have indicated that spring wheats and barleys develop more severe infections than winter wheats. However, part of the differences in susceptibility noted in the field can undoubtedly be accounted for on the basis of temperature and soil-moisture differences during the winter and spring growth periods.

LIFE HISTORY OF HELMINTHOSPORIUM SATIVUM

No perfect fruiting stage has been discovered in connection with *Helminthosporium sativum.* The organism produces conidia profusely on the host and on most culture media. It thrives as a saprophyte on straw and old stubble and sporulates abundantly on these materials. Owing to the profuse development of conidia it is very difficult to determine whether the mycelium survives the winter. Numerous soil-inoculation experiments in the fall at Madison, Wis., showed that the organism survives the winter in the soil and will produce infection on wheat plants in the spring.

The fungus lives for long periods under laboratory conditions. The writer has carefully plated infected barley seed over 2 years old and found the mycelium still alive in a high percentage of the seed. Germination tests of conidia from barley leaves which had been stored in a herbarium at Madison, Wis., for nearly three years also have been made by him, and it has been found that a low percentage of the spores germinated on agar plates.

The writer has reported previously (*45*) that the conidia of *Helminthosporium sativum* remain in a dormant state when placed in a large quantity of water. It has been found that the conidia will germinate freely when removed from the water and put on agar plates or in small quantities of water, such as a hanging drop. The writer has had tap-water and distilled-water suspensions of this organism in the laboratory for eight months, during which time practically no germination took place. During this period a high percentage of the spores germinated when removed from the water and placed on agar, and not until the end of the eighth month did a marked decrease in viability become apparent.

According to Stevens (*67*) *Helminthosporium sativum* tends to produce new races ("saltations") when grown on artificial media. He states that the variant or saltating portions of the colonies frequently show morphological characters which differ widely from the original colony. He says, further, that these variants retain their characters and sometimes resaltate when transferred. Christensen (*13*) states that he has found at least four physiological forms of *H. sativum.* These forms are based on cultural and morphological differences primarily, and although he says that the four strains showed some differences in pathogenicity when applied to a susceptible host, his evidence does not seem to warrant a definite statement concerning genetic differences in virulence between the strains he studied. In connection with Christensen's work it would be of interest to know whether he found "saltation" in his cultures of *H. sativum.* His Plate 5 gives a suggestion of differentiating sectors in the colonies of his physiologic Forms I and III, similar to the sectors shown by Stevens (*67*), but there seem to be no recorded observations in Christensen's paper concerning the occurrence of "saltation" among the strains he studied.

CONDITIONS INFLUENCING THE DEVELOPMENT OF HELMINTHOSPORIUM FOOT-ROT

Data have been published previously (*45*) on the influence of soil temperature and moisture on the development of seedling infection and early stages of foot-rot. In general, these results show that fairly high soil temperatures (28° to 32° C.) and high soil moistures (55 to 65 per cent moisture-holding capacity) favor infection. These studies indicated that the optimum temperature for infection of seedlings and young plants of Marquis wheat and Hanna barley is near 28°, whereas for Harvest Queen wheat the optimum is near 32° C. The general summary of the results obtained in the soil-temperature studies is represented by the curve in Figure 2. The results of a combined soil-temperature and moisture experiment indicate that the temperature optimum is fairly stable when soil moisture is varied. However, when soil temperature was varied the moisture optimum seemed to vary. At high soil temperatures high soil moistures seemed most favorable for infection, whereas at low soil temperatures infection seemed to increase at lower soil moistures. Extremely low soil moistures were unfavorable for infection at all temperatures, and at extremely high and low temperatures the moisture curves for infection were very irregular. While this combined experiment was preliminary in nature, the results obtained were consistent both within themselves and with the data obtained in the independent temperature and moisture experiments. A preliminary experiment in which alternating soil temperatures were employed gave essentially the same amount of infection as an experiment conducted at the same time but in which a constant temperature equivalent to the mean of the fluctuating temperatures was used.

TABLE 4.—*Influence of temperature on the growth of Helminthosporium sativum isolated from barley and from wheat*

[Growth determined by diameter of colonies]

Series	Temperature (° C.)		Diameter of colonies (mm.)			
			Fungus from barley		Fungus from wheat	
	Range	Mean	A	B	A	B
No. 1, 6 days' duration	6–8	7.4	0	0	----------	----------
	10–13	11.5	5	6	----------	----------
	15–17	15.9	15	13	----------	----------
	20–23	21.1	21	----------	----------	----------
	24–26	25.1	70	72	----------	----------
	30–33	31.7	26	22	----------	----------
	34–36	35.0	7	5	----------	----------
	37–40	38.7	0	0	----------	----------
No. 2, 9 days' duration	7–9	8.0	8	8	4	----------
	8–13	10.5	35	34	40	35
	16–19	17.5	70	75	75	75
	18–22	20.0	87	90	90	----------
	24–25	24.5	90	90	90	----------
	28–33	30.5	----------	60	28	22
	35–36.5	35.7	0	0	0	0
	38.5–39	38.7	0	0	0	0
No. 3, 8 days' duration	7.5–10	9.2	10	11	12	15
	12–13.5	12.7	29	38	30	37
	15–17.5	16.2	49	51	41	35
	20–21	20.5	68	56	49	----------
	25–26.5	25.7	67	59	85	79
	29–31	30.0	54	53	80	----------
	34–37	35.5	2	----------	0	2

Experiments (*45*) dealing with the influence of different dates of sowing in the field show that early fall seeding favors infection. Although field experimental evidence is lacking in regard to the influence of seeding on infection in spring wheats, from the evidence on fall seeding it would seem that late spring sowing would tend to increase infection. However, further study is required before this conclusion can be drawn definitely. On a basis of temperature studies with the parasite, Christensen (*13*) concluded that early spring sowing would be unfavorable for seedling infection. However, it should be pointed out that the optimum temperature for the growth of a parasite is not necessarily an index to the favorable temperature for disease development, as shown in previous work with several parasites and diseases.

As pointed out earlier (*43*, *45*), the optimum temperature for growth of the organisms used in the writer's infection studies is near 24° C. Although the fungus sporulates more abundantly at the optimum temperature for growth, sporulation is not seriously hindered even at the very high temperatures or at the very low temperatures. In all cases the organism was grown in the dark in Petri dishes of uniform size containing 20 cubic centimeters of potato-glucose agar made up to a reaction of +10 Fuller's scale. The mycelium from young single-spore cultures was transferred with blocks of agar about 3 millimeters square to the center of each of the Petri dishes, and the dishes were placed in chambers which, in turn, were placed in water-bath incubators held as near the desired temperature as possible. The data obtained from these experiments are given in Table 4.

Stevens (*67*) reports one experiment dealing with the influence of temperature on the growth of *Helminthosporium sativum* which indicated that the optimum temperature is near 25° C. Paxton (*54*) reports that the optimum temperature for growth is near 30° C., but does not state the number of experiments on which this conclusion is based.

The variations between the results obtained with presumably the same species of fungus might be explained on a basis of some strain differences. However, as the writer has obtained variations in the optima of different experiments he feels that experimental error may be the most logical explanation for the variations reported.

CONTROL OF HELMINTHOSPORIUM FOOT-ROT

While exact control measures have not been worked out for this disease, there are certain general recommendations which may be made. Since the spores of the fungus are carried on the seed, the ordinary methods of surface disinfection will control infection from this source. This method, however, is not likely to bring satisfactory results in most cases, because much primary infection of seedlings originates from mycelium borne internally in the seed and also from the fungus which persists in the soil.

Practically no work has been done to determine the best method for killing the mycelium of *Helminthosporium sativum* in wheat seeds. Atanasoff and Johnson (*3*) found that subjecting barley seed infected by this fungus to a dry-heat treatment (95° to 100° C.) for 30 hours practically controlled primary seedling infection when the treated seed was sown in uninfested soil. Their experiments were extended to wheat seed to determine the effect of these high temperatures on germination, and they found that good viable seed withstood the treatment surprisingly well. Certain of the newer organic mercury compounds which have been used (*59, 69*) to treat cereal seed seem to control or reduce the injury produced by certain parasites occurring in the seed, but in no case have these treatments been used to determine their control value for the disease caused by *H. sativum.* In general, seed treatments will tend to reduce the extent of primary infection, but they will not control infection when the parasite occurs in the soil. Since the latter condition generally exists when the disease is prevalent, effective control measures must include the consideration of the soil phase. As in the case of seed-treatment methods, however, very little has been done to combat the disease from the standpoint of soil infestation.

The application of general sanitary measures should control the disease to some extent, but just what success may be expected in this direction can not be predicted at this time. As pointed out earlier in this bulletin, the fungus apparently persists for a considerable period in the soil, even though the land may lie in summer fallow. Just what influence different cropping systems may have on the disease can not be stated until further work has been done along this line. Preliminary experiments indicate that the growth of the fungus used by the writer is favored by a neutral to slightly acid medium, but no information is at hand concerning the influence of soil reaction on the development of the disease. The influence of various fertilizers on the development of the disease is likewise undetermined.

Hayes and Stakman (*28*) have carried out breeding experiments with several varieties of barley and have obtained several strains which show resistance to the infection by *Helminthosporium sativum*. Since their studies were confined to foliage infection, it is of interest to know whether resistance to this type of infection is correlated directly with resistance to root and culm infection. So far as known, no genetic studies have been reported in connection with the resistance of wheat to infection by this parasite.

General control measures may be summarized as follows:

(1) The use of seed from badly infected fields should be avoided.

(2) The use of seed showing much black-point should be avoided.

(3) The ordinary seed treatments as used for the smuts will kill surface-borne spores.

(4) Late sowing of winter wheat tends to reduce infection.

(5) Continuous cropping with wheat, rye, and barley should be avoided. The indications are that corn, oats, and nongrass crops are safe to include in rotations.

(6) Poorly drained land should be avoided.

AN UNIDENTIFIED FOOT-ROT FOUND IN THE PACIFIC COAST STATES

During the past five years a foot-rot has appeared in a number of wheat fields near Spokane, Wash., and a similar disease has been found in the vicinities of La Grande, Oreg., and Red Bluff, Calif. After these outbreaks were called to the writer's attention by pathologists and others in the States mentioned, several field observations were made and limited experimental studies carried on. However, owing to the pressure of other problems it has not been possible to develop these investigations to a point which might be desired. Preliminary results of some of the cooperative experiments conducted in Washington have been published (*29*).

Although the foot-rot occurring in the three locations just mentioned appears to be distinct from take-all and other foot-rots of unknown cause appearing in America, it is possible that it is an unusual manifestation of some of these maladies. In some of the fields observed plants have been found which show the same symptoms as those produced by *Ophiobolus graminis*, and it would not be surprising if this fungus should later be found to cause at least part of the trouble in question. On the other hand, there are indications that other fungi may be capable of producing symptoms very similar to those produced by *O. graminis*, and until studies on other parasites have been completed too great stress should not be placed on macroscopic disease characters.

DESCRIPTION OF THE DISEASE

FIELD APPEARANCE

This foot-rot frequently gives the same general field appearance as take-all, but when the attack takes place late in the growing season the nearly mature plants show a greater tendency to break over at the base, causing large areas of wheat to lodge completely, as shown in Plate V, *A* and *B*.

DISEASE SYMPTOMS

Owing to rather limited studies, it is not possible at this time to describe the appearance of seedlings and young plants affected by this disease. During the preheading and later stages of development the diseased plants usually show various degrees of root and culm rotting. Upon endeavoring to pull diseased plants from the soil they often break away from the crown or the roots, and the bases of the culms and the roots show a brown to black coloration resembling a charred condition produced by fire. A mycelial plate somewhat similar to that produced by *Ophiobolus graminis* has been found associated with this disease rather frequently, but in many cases this plate tends to be brown rather than black in color, and it seems to be somewhat less extensive on the plant than is the case with the plate produced by *O. graminis*. Another difference which seems apparent between take-all and this foot-rot is that the basal discoloration and rotting seem to extend farther up the stems of plants affected by the foot-rot in question. This foot-rot seems to cause a collapsing of the cells at the base of the culm. These tissues contract (Pl. V, *C*), become brittle, and the stems break over, causing general lodging of the affected plants in infested areas. This condition has been recorded by Delacroix (*17*), and the writer has also noted it in connection with take-all, in which case it seems to be exceptional rather than typical. The writer has never noted this condition associated with the Helminthosporium foot-rot.

In general, the brown coloration associated with this foot-rot tends more toward black; it seems to be more diffused and to penetrate the tissues at the base of the culm more completely than the browning caused by *Helminthosporium sativum*. Brown-colored elliptical lesions with light-colored centers are frequently found on the diseased plants, but these lesions are larger than those produced by *H. sativum*, and upon plating such lesions *H. sativum* never has been obtained. However, a uniform type of sterile fungus has been obtained very regularly by Hurley Fellows, who is associated with the writer in these studies.

CAUSE OF THE DISEASE

The cause of this foot-rot has not been determined. It has been suggested that frost and general winter injury are the prime causes, but the evidence in hand indicates that these factors may act only as contributing factors rather than as direct causes of the disease. Several fungi have been found associated with the trouble, but their exact relation to the disease is not known. In 1919 a small number of mature perithecia of *Leptosphaeria herpotrichoides* De Not. were found[13] on diseased wheat plants collected by the writer near Spokane, Wash. In 1921 he (*47*) found *Wojnowicia graminis* (McAlp.) Sacc. and D. Sacc. (Pl. VI, *A* and *B*) associated with the disease as it occurs near La Grande, Oreg. This organism has been found in that region each year since the first observation was made. In 1923 H. Fellows found this organism associated with diseased plants near Spokane, Wash. Several sterile fungi have been isolated from the tissues of diseased plants, but there seem to be two prevailing forms in the Spokane and La Grande districts, one of which predominates and resembles the mycelial growth of *W. graminis*, the former resembling that of *L. herpotrichoides*.

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[13] This fungus was identified by Mrs. Edith Seymour Jones and the writer.

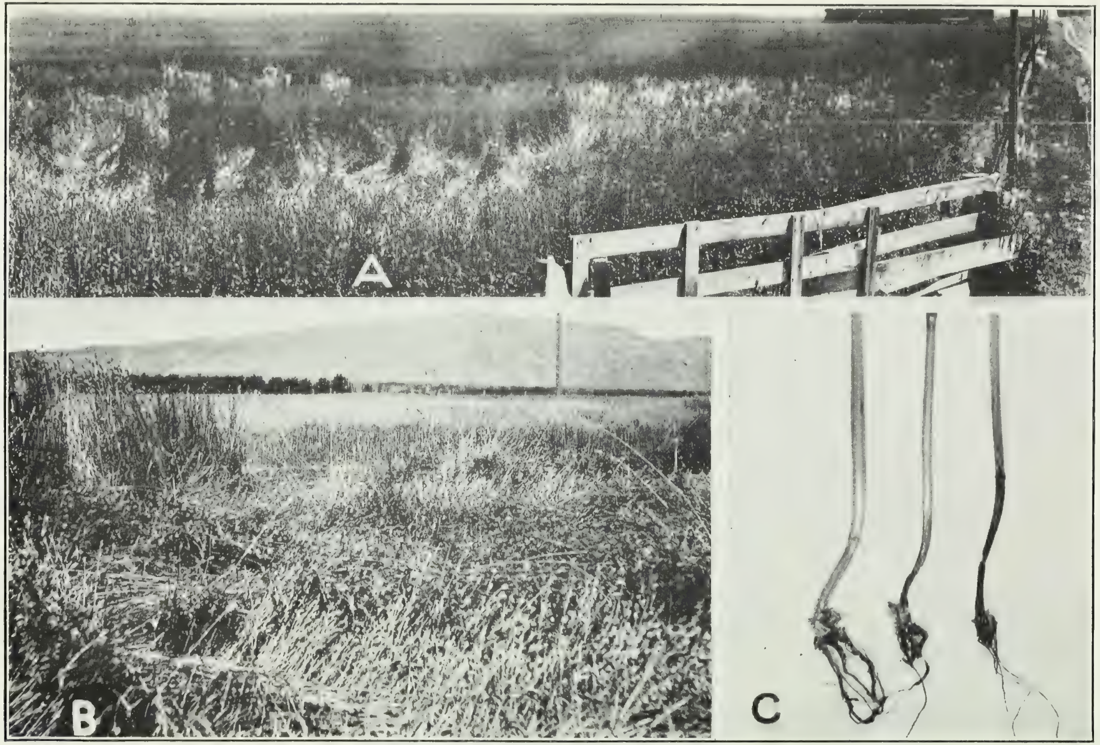
In Europe *Leptosphaeria herpotrichoides* is considered an important wheat parasite, and certain workers (*50*) have considered this organism to be the chief cause of foot-rot as it occurs on the Continent. Mangin (*50*) and Delacroix (*17*) carried out inoculation experiments with the ascospores of this organism, and their results indicate that the fungus is parasitic on wheat. In fact, Foëx and several others seem convinced that the organism is an important wheat parasite. According to Mangin (*50*) and Foëx (*22*) *L. herpotrichoides* causes a characteristic breaking over of the affected plants, and from the work of Foëx it seems that this fungus tends to extend its attacks somewhat higher above the soil line than is commonly done by *Ophiobolus graminis*. Doctor Foëx has told the writer that *L. herpotrichoides* causes rather large black to brown colored elliptical lesions on the lower part of the culms. These seem to be similar to those associated with the western foot-rot under discussion.

The writer has carried out inoculation experiments with *Wojnowicia graminis*, and the organism has been found to be slightly pathogenic on wheat seedlings. However, further studies are necessary before it will be known just how aggressive this parasite may be under various environmental conditions and what rôle it may play in connection with the foot-rot under discussion and with other foot-rots with which it has been found associated. As pointed out previously (*47*), this organism has been found associated with *Ophiobolus graminis* in Arkansas and Kansas. It has also been found associated with *Helminthosporium sativum* and several species of Fusarium in Kansas. Kirby (*39*) has recently reported its presence on diseased wheat in five counties in New York State. McAlpine (*41*) first found this organism on wheat in Australia. He noted that it was frequently associated with *O. graminis*, and he was strongly inclined to look upon it as the pycnidial form of *O. graminis*. However, as stated in a previous publication (*47*), cultures of these forms appear entirely different in growth and mycelial characteristics and in the pigmentation of the media. Such differences make it doubtful whether there is a genetic connection between these two forms.

Dana (*15*) has reported a foot-rot occurring in several counties in Washington. (Table 5.) From his description it would seem that the trouble is similar to take-all, and in certain particulars it resembles that on wheat in Spokane County, Wash. He reports finding a Rhizoctonia associated with some of the diseased plants he collected.

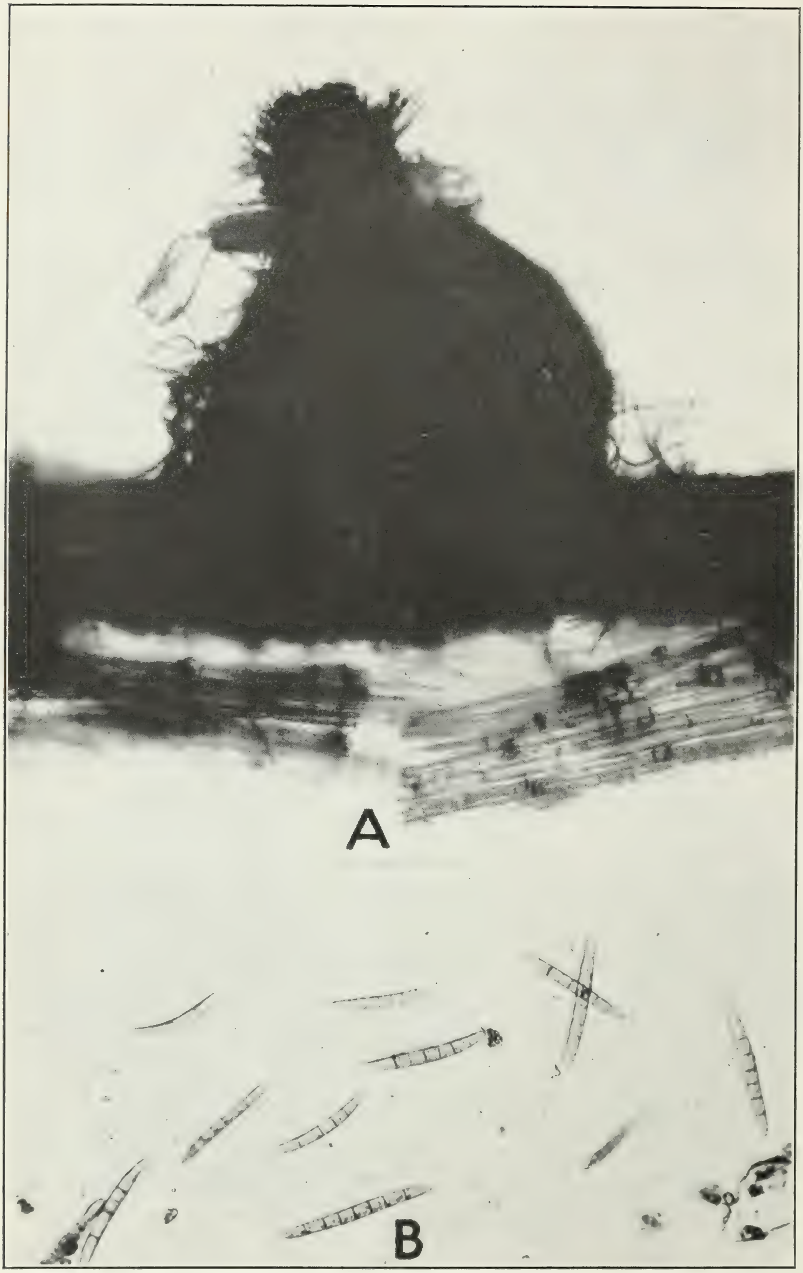
OTHER FOOT-ROTS

Reports are frequently received from various parts of the country stating that a foot-rot is damaging the wheat crop. In many instances complete data are not given, and it is impracticable to follow up all such cases with a field inspection. When possible, diseased plants are requested and plate-culture studies are made to determine the organisms which may be associated with the diseases. Table 5 shows the distribution of the undetermined foot-rots in so far as information is available.



WHEAT AFFECTED WITH A FOOT-ROT

A and *B*, Winter wheat near La Grande, Oreg., in 1923 affected by a foot-rot of undetermined cause (photographed by Hurley Fellows); *C*, similar or identical foot-rot on wheat plants from Spokane, Wash., in 1922. Left plant healthy, others diseased



WOJNOWICIA GRAMINIS ON WHEAT

A, Pycnidium from under the basal sheath of a winter-wheat plant showing symptoms resembling those of take-all, showing fragment of old leaf sheath on neck of pycnidium, ×135; *B*, pycnospores, ×525

TABLE 5.—*Distribution of miscellaneous wheat foot-rots in the United States*

[The sources of information for certain items are indicated as follows: *Reports of the Office of Plant-Disease Survey, United States Department of Agriculture; †A. W. Henry (*30*); ‡=McKinney and Melchers (*48*); §McKinney and Johnson (*47*); ‖B. F. Dana (*15*)]

Year	State and county	Organism associated	Collector	Organism identified by—
	CALIFORNIA			
1920–21	Tehama	Unknown	County agent and the writer.	
	IDAHO			
*1920	Bonner	do	C. W. Hungerford	
*1920	Latah	do	do	
*1920	Nez Perce	do	do	
*1920	Jefferson	do	do	
*1920	Minidoka	do	do	
†1922	Fremont	Sclerotium rhizodes	Unknown	Office of Pathological Collections, U. S. Department of Agriculture.
	KANSAS			
*1921	Ellis	Unknown	L. E. Melchers	
‡1921	Saline	do	do	
*1920, 1922	McPherson	do	do	
*1922	Rice	do	do	
*1920	Rawlins	do	do	
*1920	Cherokee	do	do	
*1920	Labette	do	do	
*1920	Montgomery	do	do	
*1922	Sedgwick	do	do	
§1921–1923	Dickinson	Wojnowicia graminis	A. G. Johnson, L. E. Melchers, and the writer.	A. G. Johnson and the writer.
1923	Riley	do	L. E. Melchers and the writer.	The writer.
‡1921	Cheyenne	Unknown	L. E. Melchers	
	KENTUCKY			
*1921	Logan	Helminthosporium sp.	W. D. Valleau	W. D. Valleau.
*1921	Christian	do	do	Do.
	MICHIGAN			
*1919	Van Buren	Unknown	G. H. Coons	
	MINNESOTA			
*1922	15 counties	do	Several collectors	
	NEW YORK			
*1917	Tioga	do	Charles Chupp	
*1923	Five counties	Wojnowicia graminis.	R. S. Kirby	R. S. Kirby.
	OKLAHOMA			
*1920	Garfield and others.	Unknown	C. D. Learn	
*1921	Beaver	do	Robert Stratton	
*1922	Several counties	do	do	
*1923	Woodward	Helminthosporium sativum.	L. F. Locke	The writer.
*1923	do	Helminthosporium tetramera n. sp.	do	Do.
	OREGON			
*1914	Linn	Unknown	H. S. Jackson	
1921–1923	Union	Wojnowicia graminis and several sterile fungi.	Several collectors	H. Fellows and the writer.
*1921	Jackson	Unknown	do	
*1921	Benton	do	do	
*1921	Washington	do	do	
*1921	Umatilla	do	do	
*1921	Wasco	Probably Ophiobolus graminis.	H. P. Barss	
	TENNESSEE			
*1922	Unicoi	Unknown	C. D. Sherbakoff	
*1922	Greene	do	do	
*1922	Cocke	do	do	

TABLE 5.—*Distribution of miscellaneous wheat foot-rots in the United States*—Continued

Year	State and county	Organism associated	Collector	Organism identified by—
	UTAH			
*1922	Morgan	Helminthosporium sp.	B. L. Richards	B. L. Richards.
*1922	do	Rhizoctonia sp	do	Do.
	VIRGINIA			
*1919	Page	Unknown	F. D. Fromme	
*1919	Rockingham	do	do	
	WASHINGTON			
‖1918–19	Thurston	do	County agent	
‖1918	Cowlitz	do	do	
‖1918	Snohomish	do	do	
1919–1923	Spokane	Leptosphaeria herpotrichoides.	F. D. Heald and the writer.	Mrs. E. S. Jones and the writer.
1923	do	Wojnowicia graminis.	H. Fellows	H. Fellows and the writer.
*1919	Whatcom	Unknown	F. D. Heald, B. F. Dana, and G. L. Zundell.	
*1919	Pierce	do	do	
*1919	Grays Harbor	do	do	
*1919	Lewis	do	do	
*1919	Clarke	do	do	
*1919	Klickitat	do	do	
*1919	Clarke	do	do	

For the past four years a severe foot-rot has occurred in the winter-wheat fields of Oklahoma. The writer has received many specimens of diseased plants from Robert Stratton, of the Oklahoma Agricultural Experiment Station, and from L. F. Locke, of the Woodward (Okla.) Field Station of the Office of Dry-Land Agriculture Investigations, Bureau of Plant Industry, U. S. Department of Agriculture. In many cases plants have shown the symptoms of take-all, including a white-head condition, but thus far no perithecia of *Ophiobolus graminis* have been found. In 1923 a considerable quantity of diseased plant material from the vicinity of Woodward, Okla., was plated by the writer, and *Helminthosporium sativum* was obtained in a number of cases. In addition, an undescribed hypomycetous fungus, as previously reported (*46*), was also obtained from a limited number of diseased plants. Part of the trouble occurring in Oklahoma is attributable to *H. sativum*, but it seems rather doubtful whether this fungus is the only parasite involved. In many ways this trouble is similar to that occurring in parts of Kansas where *O. graminis* fruits sparsely and is found in combination with *H. sativum* and other fungi. In a former publication the writer (*46*) pointed out that this previously undescribed fungus from Oklahoma is pathogenic on winter wheat. Under experimental conditions the organism attacks the roots and the base of the stem, causing an injury similar to that produced by *H. sativum*. However, it seems doubtful whether this organism is an aggressive parasite. The exact relation of this fungus to the Oklahoma foot-rot can not be predicted, and it is not known how widely distributed this fungus may be.

This fungus is named and described as follows:

Helminthosporium tetramera n. sp.

Conidiophores, dark olivaceous to brown, very irregular. Simple or compound, septa 5 to 50 microns apart. Conidia are produced at irregular distances from the bases of the conidiophores (fig. 5).

Conidia chiefly 4-celled, borne in clusters of 2 or 3 to 50 or more, dark olivaceous to brown, usually rather symmetrical in shape, tapering toward the rounded ends (fig. 5). Length measurements range from 20.4 to 40.8 microns, but only a very small percentage of the spores possesses the extreme dimensions. Of the spores measured 48 per cent were from 30.6 to 34.0 microns long, 30.6 microns being the most common length. The width measurements range from 8.5 to 20.4 microns, and, as in the case of the length measurements, only a small percentage of the spores possesses the maximum and minimum width dimensions. The diameters, however, seem to vary considerably less than the length measurements, as 74.2 per cent of the spores measured were 10.2 to 13.6 microns wide, 13.6 microns being the most common width. Mature conidia are practically always 4-celled. Even in the case of the longer sizes it is exceedingly rare to find conidia having more than four cells. The spore walls are not constricted at the septa. There seems to be very little, if an, change in spore characters when the fungus is cultured artificially.

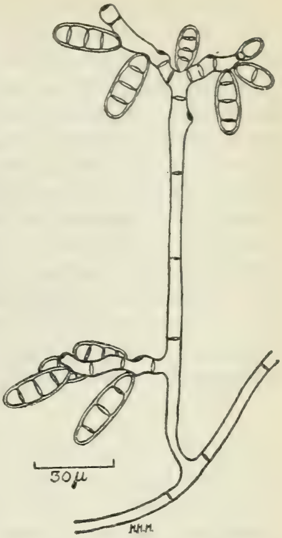


FIG. 5.—Hyphal thread, conidiophore, and conidia of *Helminthosporium tetramera*

On potato-glucose agar the fungus produces numerous long simple or branched sclerotia. These are made up of a hard white pseudoparenchyma with an outer black layer or rind. Many hyphal strands develop from this rind, but no conidia have been found on them.

Associated with a foot-rot of winter wheat, collected near Woodward, Okla., in the spring of 1923.

OTHER FUNGI CAPABLE OF CAUSING FOOT-ROTS

In addition to the parasites which have been discussed, certain other organisms are constantly referred to in the literature dealing with the foot-rot diseases of wheat. European writers (*23*, *70*) have long considered *Ophiobolus herpotrichus* an important wheat parasite, and Frank (*23*) is of the opinion that this organism is the chief cause of wheat foot-rot in certain German Provinces. This organism has not yet been reported in America.

Various European papers refer to several species of Fusaria in connection with foot-rot, and in this country Atanasoff (*1*) reported that the Fusarium stage of *Gibberella saubinetii* will cause a foot-rot on wheat. The same writer (*2*) published further on the Fusarium diseases of cereals and claims that several species of this genus cause foot-rot of wheat both in Europe and America. According to Johnson and Dickson (*34*) *G. saubinetii* is widespread throughout the principal wheat regions of this country and causes considerable injury to the heads and grain, but in spite of this wide distribution and damage to the aboveground parts the writer has not found it associated to any great extent with other foot-rots he has studied. In certain localities this parasite has been found associated with *Helminthosporium sativum* and *Ophiobolus graminis*, but it appears that the last-mentioned organisms were the chief causes of the foot-rot conditions under study.

Isolation studies by Beckwith (*4*), Bolley (*10*), and Stakman (*65*) have shown that several other genera of fungi are associated with culm rots and root rots. Among these genera species of Colletotrichum, Alternaria, and Macrosporium seem to be common, and the studies of these workers indicate that some of these fungi are parasitic on wheat seedlings. Recently Hungerford (*33*) reported *Sclerotium rhizodes* associated with a wheat disease occurring in Idaho. The field and plant symptoms associated with this trouble seem to be similar in some particulars to those manifested by the foot-rots, and it may be that this organism will be found to cause the disease in question. According to Haskell and Wood (*27, p. 207*), B. L. Richards has reported to the Office of Plant-Disease Survey that a species of Rhizoctonia is associated with wheat foot-rot in Morgan County, Utah. There is no statement, however, as to the pathogenicity of this fungus on wheat.

DISCUSSION

The foot-rot diseases of wheat are rather widespread in America, causing crop losses of economic importance in several of the principal wheat districts. Although the studies which have been carried on by numerous investigators have thrown considerable light on these diseases, it is certainly evident that they have done little more than to assist in defining some of the problems and to convince some of the students of the soil and of cereals that soil fungi are in many cases the limiting factors in wheat production. As the study of these problems progresses, it becomes increasingly evident to the writer that the general suggestion made by Bolley (*10*) that the low wheat yields in many of our principal wheat districts can not be accounted for chiefly on the basis of low soil fertility deserves very careful consideration. It seems evident that any constructive program of investigation for the purpose of increasing wheat yields must include a study of wheat diseases caused by the parasites infesting the soil.

In attacking plant-disease problems it is generally accepted that the causal agents must be studied independently under controlled conditions in order that an accurate understanding of the problem in hand may be obtained. This method has led to the development of refined laboratory methods whereby parasites may be cultured and kept free from contaminating organisms and whereby the environmental influences also may be kept as constant as possible or varied at will when such parasites are studied independently or in relation to the development of disease. Although these refined methods are highly essential and important in connection with obtaining certain knowledge, it must be recognized that investigators too frequently are prone to confine their disease studies to these ultrarefined methods instead of supplementing them with the somewhat less refined ones which are more comparable to the conditions under which the plant grows in nature. Several cases are on record where organisms have been classed as cereal parasites on the basis of inoculations made on plants grown in the rag-doll seed tester or in agar contained in test tubes. In some cases such experiments have not been followed up by soil-inoculation studies, or if such studies have been made they were of a very minor nature, and the final conclusions were based primarily on results obtained by the more artificial technique. The writer has made use of the agar and test-tube method to a limited extent in connection with infection studies, but experience indicates that it is of questionable value in establishing the pathogenicity of organisms as they occur in the field. Under test-tube conditions and the conditions obtained in a roll of cloth, such as a rag-doll seed tester, the wheat seedling is at a decided disadvantage, whereas the fungus has an ideal opportunity to attack the plant. Even in the case of carefully planned soil-inoculation experiments it is extremely difficult at times to obtain results which can be interpreted and compared satisfactorily with conditions occurring in nature. The writer has demonstrated repeatedly that the amount of inoculum introduced into soil greatly influences the number of plants which become infected and the severity of the infection on the plants attacked. Up to a certain point large amounts of inoculum have always caused an increased amount of infection, which might easily be confused with the factor of virulence. This relationship was observed repeatedly in the work with *Actinomyces scabies* (*36*), *Helminthosporium sativum* (*45*), and *Ophiobolus graminis*. When it is possible the writer introduces only the spores and mycelium of the fungus to the experimental soil, and when nonsporulating forms are used they are, when possible, increased on inert materials, such as straw and leaf mold. In some cases, it has been necessary to use cooked oat and barley grains for culturing sterile forms, but in these cases it is always the aim to avoid the addition of too much of such culture material to the soil.

In the study of the factors which influence parasitism among soil fungi, we are continually reminded that the distinction between the pathogenic and saprophytic types is very largely relative. Certain parasites are more aggressive than others, some are capable of attacking the host throughout a wider range of environmental conditions than others, and if the right conditions are obtained some of the so-called saprophytes become pathogenic. In view of these relationships it becomes strikingly evident that the mere statement that an organism is pathogenic or nonpathogenic means very little to the student of plant diseases. Information regarding the environmental conditions, the methods used, and the general conditions under which experimental or field observations are made is highly important and should be recorded.

The control of foot-rot diseases is the ultimate thing sought in the studies being carried on by the Government and State agencies. Although certain information is available on this phase, it is strikingly evident from the material presented in this bulletin that much more exact knowledge should be obtained. As these diseases are caused by soil-inhabiting parasites, it is evident that seed treatments alone can not solve the control problems. The soil is the important source of infection, and it is evident that this aspect of the problem must be given considerable attention. In order to combat this source of infection several methods are open for investigation, some of which are more practical than others.

The host may be aided in escaping infection by several methods, but the practicability of these depends very largely on the circumstances surrounding each farmer's problem. The soil-temperature studies which have been carried on with certain soil-inhabiting parasites have shown that the date of seeding may be regulated so as to assist the wheat plant in escaping infection or serious injury in case the fungus gains entrance. However, this method is not applicable in some cases, as, for example, in parts of Kansas where *Ophiobolus graminis* and *Helminthosporium sativum* sometimes appear in the same wheat fields, and in parts of Wisconsin, Minnesota, and the Dakotas where *Gibberella saubinetii* and *H. sativum* appear together. As indicated in Figure 2 (p. 13), infection by *O. graminis* is favored by fairly low soil temperatures, whereas infection by *H. sativum* is favored by fairly high soil temperatures, and on the basis of the studies reported by Dickson (*18*) the optimum soil temperature for wheat-seedling infection by *G. saubinetii* lies between the temperature optima for *O. graminis* and *H. sativum*. From these data it is evident that any arrangement of fall or spring seeding dates for the purpose of obtaining soil-temperature differences will result in very little economic benefit to the farmer when any two or more of these parasites occur together. Plainly, if the temperature conditions are not favorable for one disease they are likely to be so for one of the others, as is shown by the curves in Figure 2.

Several investigators have attempted to control foot-rots by means of special cropping and soil-tillage systems and also through the use of fertilizers and amendments. Although these methods of control have not been thoroughly developed for any of these diseases, there is good reason to believe that, in certain regions at least, they offer one of the most promising means of reducing crop losses due to foot-rots.

The development of varieties resistant to foot-rots has not been given systematic consideration by many plant breeders, and therefore very little definite knowledge on this subject is at hand. Several investigators have mentioned varieties as being resistant to certain foot-rots, but in some cases varieties said to be resistant by one worker are reported highly susceptible by another. In general, it may be stated that most wheat varieties seem to be susceptible to one or another of the foot-rots when the proper conditions for infection exist.

Numerous attempts have been made to control foot-rots by treating the soil with chemicals which kill the parasites present. In some cases the results have been successful, but in most instances the materials used were too expensive for general field use. This mode of attacking plant parasites which live in the soil has not been studied systematically. Low-priced chemicals have not been investigated, nor have the methods of application been studied. This method should be efficient for the control of such foot-rots as take-all when they are not too extensively distributed over a field. However, it appears doubtful whether this method would ever be practicable for the control of the Helminthosporium foot-rot, owing to the wide dissemination and copious occurrence of the spores of the parasite.

On the basis of our present knowledge it is clear that the control of the foot-rots depends not on one method but on several.[14]

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[14] The following publications on the wheat foot-rots were received after this bulletin was prepared for the printer:

Dosdall, Louise. Factors influencing the pathogenicity of Helminthosporium sativum. Minn. Agr. Exp. Sta. Tech. Bul. 17, 47 pp. illus., 1923.

Guyot, L. De l'existence de formes pycnidiennes chez Ophiobolus graminis, Sacc., et Ophiobolus herpotrichus (Fr.) Sacc. *In* Rev. Path. Vég. et Ent. Agr., t. 12, pp. 74–81, illus., 1925.

Seed treatments and the selection of clean seed will tend to prevent the spread and increase of the parasites.

Rotations, including a liberal use of oats, legumes, sorghums, and in some cases corn, will at least assist the farmer in obtaining a crop from infested soil.

Summer fallowing infested land in combination with certain rotations has given good results in combating take-all in Australia. Although this method has not been given a thorough trial in America, it is reasonable to believe that it should give as good results here in districts where summer fallowing is practiced. The effect of this practice on the control of other foot-rots is not definitely known, but in the case of the Helminthosporium foot-rot preliminary experiments indicate that summer fallowing has but little, if any, effect on the disease.

It is considered good practice to prevent undue accumulation of infested straw in wheat fields and to prevent the promiscuous growth of wild grasses which are parasitized by the foot-rot organisms. Infested straw should not be spread on the soil. When used as bedding for farm animals the resulting manure should be composted before being applied to the soil.

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